Weaving through the matrix:

Investigating the influence of urban land use on weaver bird movements into and out of Cape Town wetlands

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Plagiarism Declaration

I know the meaning of plagiarism and declare that all of the work in the document, save for that which is properly acknowledged, is my own.

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Date_____

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Abstract

Urbanization, a fast growing and destructive human land use, causes local extinctions, biotic homogenization and fragmentation of natural habitats. Understanding how the nature of the urban matrix affects the species residing within a city's fragmented habitats is an important founding component of urban conservation. This study investigated the influence that the urban matrix, as well as patch isolation, size and quality, had on weaver bird movement into and out of wetland sites in Cape Town, a growing city within a global biodiversity hotspot. Weaver bird movement data from 42 wetland sites were obtained through a long term mark-release-recapture project. Distance-based linear models revealed that site proximity was important as a predictor of weaver movement into and out of sites, while the site variables (wetland size, bird abundance and weaver colony size) had limited and inconclusive influence. Once the variation explained by the proximity and site variables had been accounted for, the composition of the urban matrix and the presence of rivers as potential movement corridors (measured at three spatial scales) had little influence on weaver movement. The finding that proximity (or site isolation) influences weaver movement has important implications for maintaining current landscape connectivity. Habitat isolation, resulting from further habitat removal or destruction, could be expected to reduce movements of weavers, and potentially other species, among patches of favourable habitat. Weavers are robust, vagile birds that do well in the presence of humans and may not be highly sensitive to the nature of the urban matrix. Research into how other, less resilient and vagile species respond to the degree of urbanization in the matrix between wetlands would contribute further to our knowledge of urban biodiversity in this global biodiversity hotspot.

Keywords: habitat fragmentation, passerine dispersal, urban matrix, proximity,

Introduction

Land use change resulting in habitat loss, modification and fragmentation is one of the greatest threats to biodiversity globally (Rudd et al. 2002; Prugh et al. 2008). One of the fastest growing human land uses is urbanization; since 2008, more than half of the world's 7 billion people have been living in urban areas (UN 2008). Agricultural and urban settlements account for approximately 40% of the earth's ice-free land (Ellis et al. 2010) and it is estimated that 10% of the world's coastal regions are covered by urban landscapes (Dearborn & Kark 2010).

Traditionally, conservation efforts have focussed primarily on preserving pristine, rural lands where ecosystems are functioning at a near-natural state (Dearborn & Kark 2010). However, it has become clear that the 14.3% of global land currently under formal protection (World Bank 2013) will not be sufficient in meeting global targets for biodiversity conservation (Millennium Ecosystem Assessment 2005). The ecosystem fragments within cities not only provide valuable services for city dwellers (e.g. water purification by wetlands or the intrinsic value of green spaces) but are also important habitats for many plants and animals (Rudd et al. 2002; Dearborn & Kark 2010). With so much of the world now under urban land use, it is essential to consider urban areas as conservation opportunities in themselves (Ellis et al. 2010), and studying the patterns and processes of urban biodiversity will not only aid global conservation but can also enlighten the planning of cities in the future (Pickett et al. 2011).

Cape Town, the southernmost city in Africa, is a well-known case for the need to conserve urban biodiversity (Dearborn & Kark 2010). Not only does Cape Town fall within one of the world's biodiversity hotspots, the Cape Floristic Region (CFR)(Myers et al. 2000), but the city itself is home to many endemic species including 158 plant species and two threatened frogs (Helme & Trinder-Smith 2006; Rebelo et al. 2011). The human population within the CFR is the second fastest growing of all Mediterranean regions (Rebelo et al. 2011), and most of the population resides in Cape Town (Regional development profile: City of Cape Town, 2012). This combination of human population

growth in the midst of invaluable flora and fauna implies a strong need for a thorough understanding of Cape Town's urban biodiversity.

Urbanization and biodiversity

Urbanization can be defined as "concentrated human presence in residential and industrial settings and their associated affects" (Chace & Walsh 2006). Urban development is an especially harsh human land use practice (McKinney 2002; Shochat et al. 2006). It involves an initial and extreme disturbance followed by continued maintenance and spread of the artificial environment and unlike other land uses, it offers limited potential for restoration and rehabilitation (McKinney 2002; Meffert & Dziock 2013). Urbanization is associated with, among other things, high rates of local extinctions, altered community compositions and reduced landscape heterogeneity (McKinney 2002; Dures & Cumming 2010; Meffert & Dziock 2013). Singapore is an extreme example of the impacts of urbanization as urban development left the region with just one quarter of its original native species (Dearborn & Kark 2010). Such high levels of species loss are mostly attributable to the removal of natural vegetation and the consequent reduction of suitable habitats (McKinney 2002). Cities pose an interesting set of opportunities for conservation biologists; not only as systems in which to gain insights into the impacts of habitat loss and fragmentation (which can then be applied to other systems), but also as tools to connect people to the environment and improve awareness of the importance of local conservation (Dearborn & Kark 2010).

Not only does urban development lead to local extinctions and biotic homogenization (McKinney 2006), but like other human land uses, it fragments natural habitats (Savard et al. 2000; Grimm et al. 2008; Faeth et al. 2011). Habitat fragmentation involves a significant reduction in habitat area resulting in several smaller patches, with a reduced total area, separated from each other by a matrix habitat distinctly different from the original (Saunders et al. 1991; Fahrig 2003). Understanding how the spatial arrangement of these remnant patches affects species persistence

and population dynamics is of great interest to ecologists as so many of the world's biota now reside in fragmented landscapes (Ricketts 2001; Ewers & Didham 2006; Dures & Cumming 2010).

The importance of connectivity

Fragmentation reduces the extent of available habitat and isolates remaining habitat patches (Saunders et al. 1991). A wide range of ecological evidence (e.g. species-area curves, metapopulation models, and the theory of island biogeography) suggests that smaller, more isolated habitat patches will host fewer species and smaller populations than will larger, better-connected patches, and this well-supported principle underlies the drive to avoid further habitat fragmentation (Prugh et al. 2008). Isolated populations are at risk of falling victim to combinations of demographic, environmental and genetic forces that act in concert to create extinction "vortices" that jeopardise their long-term survival (Fahrig & Merriam 1985; Crooks & Sanjayan 2006).

Connectivity was defined by Taylor et al. (1993) as: "the degree to which the landscape facilitates or impedes movement among resource patches". Maintaining a degree of connectivity in a fragmented landscape is crucial for the survival and persistence of isolated populations because without it, naturally ranging animals may not be able to move between foraging and breeding sites or emigrate from their natal patches (Crooks & Sanjayan 2006). Movement between patches is important for the exchange of genetic material: without gene flow, isolated populations may become less resilient to novel threats (i.e. diseases) and could experience the negative effects of inbreeding depression (Simberloff & Cox 1987; Crooks & Sanjayan 2006). From an evolutionary perspective, gene flow forms the foundation of adaptation to a changing environment, allowing species the opportunity to respond to an uncertain future (Crooks & Sanjayan 2006). In an urban context, species may occur entirely as isolated populations in fragmented patches, so it is essential for their persistence that a sufficient level of connectivity is maintained.

Connectivity as an animal's ability to disperse through the landscape

From the perspective of a single species, connectivity is not only dependent on the structure and composition of the landscape, but also on the nature of the individual and how it perceives the landscape (Haddad et al. 2003). Fagan and Calabrese (2006) stated that, "connectivity, regardless of the spatial scale on which it is defined, is a species-dependent trait". In this regard, connectivity can be viewed as either structural or functional. Structural connectivity relates to the physical composition of habitat types in a landscape and functional connectivity incorporates the behaviour of the individual and how it responds to the physical structure (Crooks & Sanjayan 2006). The functional connectivity of the landscape relates to the way in which the landscape impedes or assists an animal's dispersal between habitat patches. Dispersal, broadly defined as movement between patches, can be viewed in three distinct stages; emigration (movement out of a patch), navigation through the intervening "matrix" (inter-patch movement) and immigration (movement into a patch) (Bowler & Benton 2005).

Dispersal can be a costly exercise as it requires an animal to leave the familiarity of its original habitat and risk moving through unknown territory in the hope of finding a new patch of equal or higher quality than the original. In order for dispersal and movement strategies to evolve, the benefits of leaving one patch and finding a new one must outweigh the costs of dispersal (Bowler & Benton 2005; Fahrig 2007). In a comprehensive review, Bowler and Benton (2005) discussed and summarised the causes and consequences of animal dispersal strategies in terms of emigration, inter-patch movement and immigration. I will focus specifically on how aspects of the landscape can influence movement into and out of habitat patches.

Dispersal and habitat patch proximity and isolation

One of the major aspects thought to influence animal movement and the associated population dynamics is the spatial arrangement and degree of isolation of habitat patches within a

matrix (Gustafson & Gardner 1996; Bowler & Benton 2005; Ewers & Didham 2006). As the distance between two patches increases, so does the risk associated with dispersal, thereby reducing the likelihood that an animal will successfully arrive at its destination patch (Bowler & Benton 2005). An animal is more likely to locate the destination patch if it is within a reasonable search radius of its home patch (Bowler & Benton 2005). Conversely, movement between nearby sites would be less risky and more likely (Bowler & Benton 2005). This observation agrees with the predictions of island biogeography and metapopulation theory that colonization rates will be higher in more connected patches (MacArthur & Wilson 1967; Hanksi 1999a) and one is therefore more likely to detect movement into and out of proximal patches than isolated ones.

Dispersal and habitat patch characteristics

The features of the habitat patch itself, such as patch size and quality, can affect animal movement into and out of it (van Langevelde 2000). Patch size is a well-studied predictor of emigration and has been found to have a negative correlation with the amount of movement out of patches (Bowler & Benton 2005). Smaller patches that hold fewer resources may not be able to support current population sizes and may therefore experience higher rates of emigration (Bowler & Benton 2005). Because larger patches are easier to find and are often preferred over smaller patches, it has been suggested that patch size is positively correlated with immigration rate (Bowler & Benton 2005). In general, larger, more connected patches are thought to experience higher movement rates than smaller, more isolated patches (Fleishman et al. 2002; Franken & Hik 2004). The influence that patch size and arrangement has on fragmented populations forms the foundation of the famous SLOSS (Single Large Several Small) debate in reserve design (Simberloff & Abele 1982). The influence of habitat size versus arrangement is very much dependent on the species in question (Simberloff & Abele 1982) and Flather and Bevers (2002) found that once a population falls below a certain persistence threshold, the importance of habitat area decreases relative to the importance of habitat arrangement.

Factors other than patch size and arrangement, such as patch ecology and population dynamics, may also influence emigration and immigration rates (Fleishman et al. 2002; Bowler & Benton 2005). The population density of the focal species could influence movement negatively or positively. Competition for shared resources when population densities are high may encourage animals to leave a patch (Bowler & Benton 2005). On the other hand, the benefits of group living, such as cooperative breeding and improved vigilance will be less in smaller populations, provide a reason to leave in search of bigger populations or to stay at the current patch if such benefits are already being realised (Bowler & Benton 2005). The presence of conspecifics may also act as a habitat quality cue to potential immigrants (Franken & Hik 2004; Bowler & Benton 2005; Fahrig 2007). Patches with higher habitat quality are likely to have more immigrants than poorer quality patches that will probably experience higher rates of emigration (Bowler & Benton 2005). If dispersal is affected by habitat quality and not just the size and arrangement of patches, managers of fragmented populations may need to consider maintaining habitat integrity especially if it is influenced by human activity (Fleishman et al. 2002). The quality of habitat patches in an urban setting can be compromised by human activities such as vegetation removal, trampling and the introduction of alien species (McKinney 2002). Dures and Cumming (2010) showed how the presence of alien species can reduce habitat quality and affect bird communities in Cape Town. Although it can often be difficult to quantify (van Langevelde 2000), habitat quality is an important aspect to consider when studying animal movement in an urban landscape.

Dispersal and the intervening matrix and movement corridors

Bowler and Benton (2005) identified that dispersal into or out of a patch could be influenced by the matrix that surrounds the patch. In fragmented landscapes, usable habitat patches are, by definition, surrounded by a matrix of less usable land (Fahrig & Merriam 1985). Island biogeography and metapopulation theory have formed the foundation for studying and conserving fragmented landscapes (MacArthur & Wilson 1967; Hanksi 1999b). Both paradigms assume that the matrix

surrounding habitat fragments is uniformly hostile and that the landscape can be viewed simply as "habitat" and "matrix" (Ricketts 2001). However, the terrestrial matrix is made up of a mosaic of land uses of varying permeability, some of which may not be as hostile as the sea in the oceanic island analogy (Gustafson & Gardner 1996; Prugh et al. 2008). The permeability of the surrounding matrix is a function of both the characteristics of the matrix, and the life history traits and habits of the focal species (Ricketts 2001; Franklin & Lindenmayer 2009). For birds, which can fly over roads and buildings, the matrix may be less of an obstacle to dispersal than it might be for small mammals, invertebrates and amphibians that face these obstacles at ground level (Croci et al. 2008). The urban matrix is typically very diverse (Faeth et al. 2011) and an animal moving through it could encounter anything from paved roads and high rise buildings to planted suburban gardens with bird baths and fruiting trees. Meffert and Dziock (2013) suggested that the matrix surrounding a patch could act as a "filter" to animals attempted to enter or leave it. If a patch is surrounded by impenetrable habitat, animals might not be able leave it as successfully or willingly as they might a patch that is surrounded by more penetrable habitat (Gascon et al. 1999; Ewers & Didham 2006; Fahrig 2007). Similarly, it might not be worth immigrating into a new patch if it is surrounded by treacherous terrain, but arriving at a site could be less risky if the immediate surroundings are more favourable (Hodgson et al. 2011). Investigating how a species responds to the matrix, as well as to patch characteristics and arrangement, will help in understanding how connected the landscape seems to the species and hence, potentially aid in conserving it (Ricketts 2001; Prevedello & Vieira 2010).

Movement corridors that join habitat patches are thought to improve connectivity in a fragmented landscape and maintaining corridors has been proposed as a conservation strategy to reduce the effects of isolation (Rosenberg et al. 1997; Fernández-Juricic 2000). A movement corridor is loosely defined as a "linear landscape element that provides for movement between habitat patches, but not necessarily reproduction" (Rosenberg et al. 1997). The presence of movement corridors around habitat patches is thought to increase animal dispersal rates in fragmented systems

(Simberloff & Cox 1987). In an experimental study in a South American temperate forest, Castellón and Sieving (2006) found that relocated Chucao Tapaculos (*Scelorchilus rubecula*) (terrestrial birds with poor dispersal ability) dispersed from patches sooner in the presence of adjoining movement corridors than from patches surrounded by unfavourable habitat. As they wind their way through the landscape, rivers, and their associated natural riparian vegetation, may act as movement corridors for animals moving between habitats (Rosenberg et al. 1997). In the urban context, the creation and/or maintenance of movement corridors such as rivers, may not only provide additional habitat, but may also improve landscape connectivity (Simberloff & Cox 1987; Beier & Noss 1998; Savard et al. 2000). In Toronto, Canada, this concept is put into practice as streams that link remnants of natural vegetation are maintained as movement corridors (Savard et al. 2000).

Studying animal dispersal

Studying animal movement presents many challenges for conservation biologists and the dispersal process for many species is poorly understood (Gustafson & Gardner 1996; Bowler & Benton 2005). Attaching GPS tracking devices to animals provides valuable information on animal movement; however this method is often limited by the size and nature of the animal as well as by the availability of funds. A less intrusive, if less informative method of tracking animal movements is "mark-release-recapture" which is particularly useful for studying the movements of small animals, like passerine birds, whose small size limits their suitability for GPS tracking (Haig et al. 1998; Craig 2010). Movement records from mark-release-recapture efforts provide a means to study animal dispersal in an urban setting that can address the interaction between animal behaviour and the landscape matrix – something that past studies often failed to do (Wiens et al. 1993). Birds in particular are an excellent group for studying the effects of urbanization as they are conspicuous and easy to monitor and, due to their specific habitat requirements, are also good indicators of habitat quality (Marzluff & Ewing 2001; Chace & Walsh 2006; Pennington & Blair 2011).

Aims and objectives

Even in untransformed landscapes, wetlands are typically scattered throughout the land and are often likened to biogeographic islands in a terrestrial sea (Whited et al. 2000; Amezaga et al. 2002). This contrast is further exaggerated for wetlands in the urban context where these oasis-like habitats are strongly influenced by the nature of the surrounding matrix (Whited et al. 2000). Wetlands are valuable features in the urban landscape, not only because they provide habitat for a variety of species, but also because they provide ecosystem services such as water purification and recreational and aesthetic value (Ehrenfeld 2000). Maintaining connectivity between isolated wetlands is a primary concern for wetland conservation and requires an understanding of how animals move between them. In this study I asked whether the urban matrix surrounding wetlands, and features of the wetlands themselves, might be affecting the movements of four weaver bird species in Cape Town, South Africa. These species are colonial breeders that frequently move between habitat patches and often associate themselves with aspects of the human environment for food as well as for nesting sites (Hockey et al. 2005; Craig 2010). Since these species are not known to be particularly sensitive to human land uses (Hockey et al. 2005; Craig 2010), I expect that their movement into and out of wetlands will not be strongly affected by the nature of the land use surrounding these habitat patches, but rather by site specific features such as proximity to other sites.

Methods

I used the weaver records from the South African Bird Ringing Unit (SAFRING) database to quantify weaver movement into and out of 42 wetland sites in Cape Town. I asked whether the movements of weaver birds into and out of a site were influenced by the proximity of a site, the features of the site itself ("site variables"), and/or the nature of the matrix and the presence of rivers around the site.

1. *Study area and species*

1.1 Study area

Cape Town is home to 3.74 million people and covers an area of 2 455 km^2 (Rebelo et al. 2011) (Fig. 1). Cape Town falls within a global biodiversity hotspot; the Cape Floristic Region (CFR)(Myers et al. 2000), which is also the world's smallest floral kingdom, and boasts high plant diversity and endemism (Rebelo et al. 2011). Although the Cape is best known for its terrestrial flora, the numerous wetlands that dot the landscape contribute greatly to Cape Town's biodiversity (Holmes et al. 2008). Little is known about the historical extent of the wetlands in Cape Town (Rebelo et al. 2011) but it is thought that much of the Cape Flats was once a system of perennial and ephemeral wetlands connected via ground water (Holmes et al. 2008). These low-lying, water-logged flat lands were largely uninhabited until the 1960s when the Apartheid government initiated the development of low density housing across the Cape Flats (Rebelo et al. 2011). To assist this development, rivers were canalized, wetlands were drained and storm water was directed into the wetlands, turning seasonally inundated wetlands into unnatural permanent lakes (e.g.: Zeekoeivlei and Princessvlei) (Holmes et al. 2008). Cape Town's wetlands are no longer hydrologically connected and have become increasingly geographically isolated as they are enveloped by the urban matrix. Despite these transformations Cape Town's wetlands are still ecologically and economically important and many fall under some level of protection (e.g. Rondevlei and Zandvlei) (Holmes et al. 2008). Cape Town's wetlands host an impressive selection of bird life and many are well known birding destinations (Petersen & Tripp 1995).

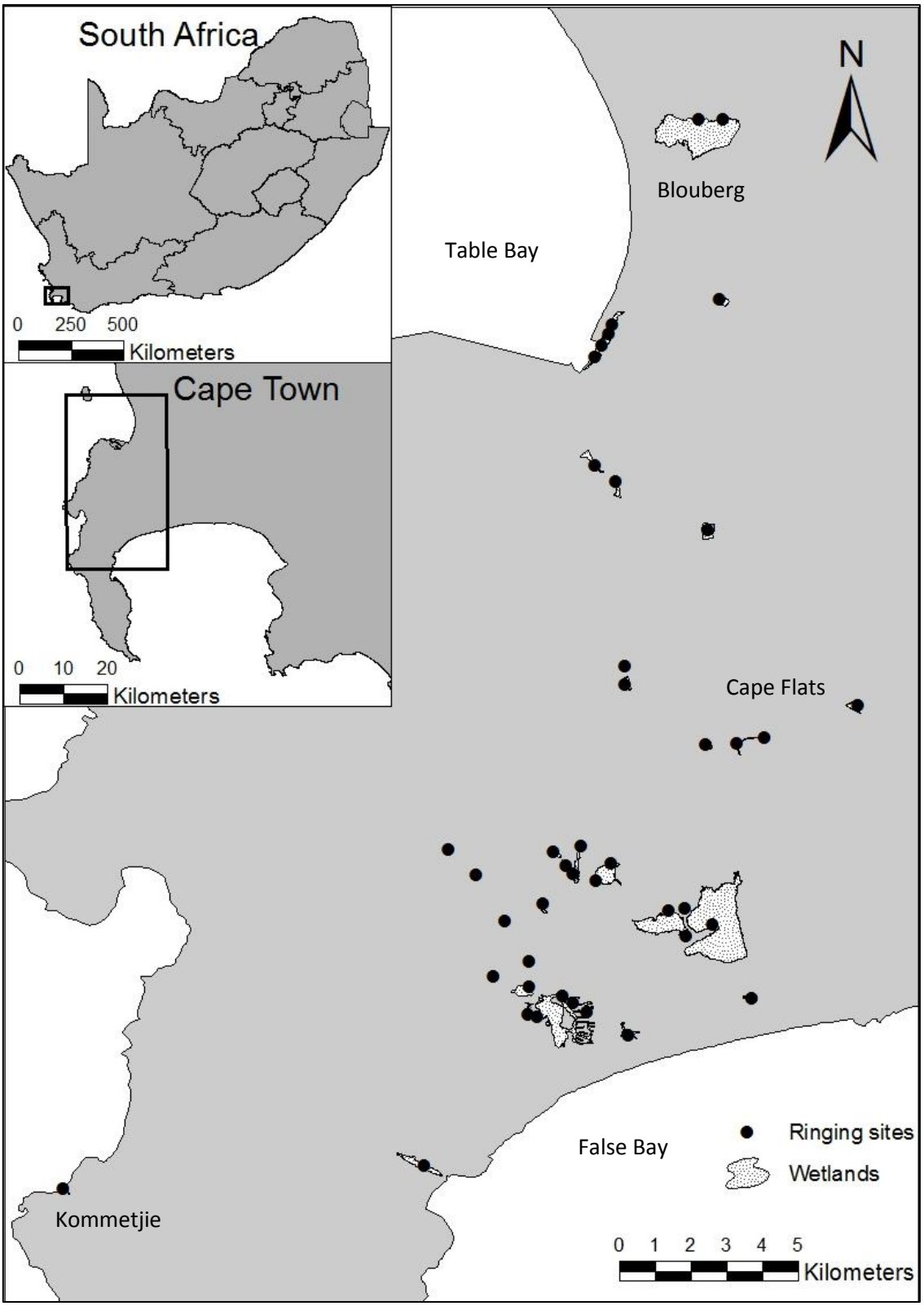

Figure 1. Distribution of ringing sites (filled circles) at selected wetlands (shaded polygons) in Cape Town. Insets indicate the location of Cape Town within South Africa and the extent of the study area within Cape Town.

1.1 Study species

The weaver bird family (Ploceidae) consists of 117 species of weavers, widow birds, queleas and bishops that are distributed throughout most of sub-Saharan Africa, South East Asia and the Indian Ocean islands (Craig 2010). The four weaver species found in the Cape Town area are the Cape Weaver (*Ploceus capensis,* Linnaeus, 1766), Southern Masked Weaver (*Ploceus velatus,* Vieillot, 1819), Yellow Bishop (*Euplectes capensis,* Linnaeus, 1766) and Southern Red Bishop (*Euplectes orix,* Linnaeus, 1758). These species are widespread in the region and common in the Western Cape (Hockey et al. 2005). All four species are colonial, polygynous breeders that nest in reeds and trees near permanent inland water bodies and river courses (Hockey et al. 2005). They all eat, to varying degrees, a mixture of seeds, other plant material, and insects (Hockey et al. 2005). These species are not threatened and are sometimes viewed as pests as they occasionally raid crops (Hockey et al. 2005). The Southern Masked Weaver is the most widespread weaver in South Africa and its fairly recent range expansion into the Western Cape has been attributed to its adaptive use of fences and alien vegetation as nest sites (Hockey et al. 2005). The Cape Weaver is also well adapted to the human environment and can be found feeding at garden bird feeders and nesting over farm dams (Hockey et al. 2005; Craig 2010). The Yellow Bishop and the Southern Red Bishop are known to become highly territorial during the breeding season (Hockey et al. 2005).

None of these species undergo a migration and are all resident and sedentary, but they do move locally between habitats (Hockey et al. 2005). The Cape Weaver in particular is known to fly direct and fast over the landscape (Fry & Keith 2004). Fraser et al. (1990) studied Cape Weaver movements in the South-Western Cape by mist netting and ringing birds at different locations. The furthest Cape Weaver movement detected was 156 km and the average distance was 30.1 km (Fraser et al. 1990). On the topic of Southern Red Bishop movement in South Africa, Craig (2010) remarked, “few move more than 100km from ringing site and such local movements, related to food availability, may be typical of many weavers”.

Because these four species display similar habitat requirements and dispersal strategies, I grouped them together in this study and explored the potential influence that the predictor variables may have on this group, the "weavers".

2. *Bird ringing and the SAFRING database*

The movement data that were analysed in this study were collected by Dr. H Dieter Oschadleus, the coordinator of the South African Bird Ringing Unit (SAFRING; see http://safring.adu.org.za/). Since 2007, a massive effort was made to capture and ring the four species of weaver birds found in the Cape Town area. The bird ringing data used for this study were collected between January 2007 and September 2013. A thorough search was conducted for weaver colonies and roost sites at likely sites in the Cape Town area (wetlands and water bodies with suitable vegetation) and once a weaver colony or roost site was found, mist nets were erected (typically in the early morning) to capture weavers, as well as other "by catch" species. GPS co-ordinates were recorded at each ringing site. Each bird was ringed with a metal ring which carried a unique identification number. This number, along with the date, site, ringer's name and species details was recorded in the SAFRING database. Many of the sites, especially those with large numbers of weavers, were visited regularly and over a long period of time, whilst others that were perhaps less accessible or had less weavers, were visited less regularly. At some of the sites, chicks in nests were ringed if they were of the appropriate age and size. Mist-netting effort was recorded at most of the sites on most occasions as "net hours" which is the length of the net used (m) multiplied by the number of hours the nets were set for. The unique number on the rings allowed birds to be identified if they were captured a subsequent time – a recapture.

2.1 Selecting appropriate sites

The database had records of weaver birds captured and/or ringed at 101 locations. However, upon closer inspection of the raw data, it was clear that many of these locations were neither appropriate nor necessary for this analysis. The following criteria were used to select sites for the analysis:

1. Sites were included only if they were associated with a wetland, water body or river course.
2. If a site was not a mist netting site (i.e.: only chicks were ringed) it was either dropped or collapsed into a nearby mist netting site at the same wetland.
3. Sites were dropped if they were not focused on a weaver colony (ie. If only one weaver was ever caught there and this weaver was never recaptured)
4. If two or more sites were essentially the same site (i.e.: if mist netting was conducted by different people who gave the same site different GPS coordinates or a different name) the sites were collapsed into one and given the coordinates of the site with the most effort.
5. If sites were very close to each other (less than 300 m) and were associated with the same wetland system then they were collapsed into one site and given the coordinates of the site with the most effort.
6. Sites that had become inaccessible were dropped or collapsed into a nearby site at the same wetland because accessibility was essential for conducting bird counts (see later).

Adhering to these criteria, the set of sites was reduced to 42, associated with 31 wetlands in the Cape Town region. The northernmost site was at Rietvlei in Blouberg and the southernmost site, 35 km from Rietvlei, was at the Bokram river wetland in Kommetjie (Fig. 1).

Bowler and Benton (2005) defined habitat patches as “areas of suitable habitat separated in space from other such areas, irrespective of the distance between them”. Although some of the sites in this study did not strictly meet this definition (in some cases a few sites are associated with the same wetland system (Fig. 1)) each site focused on a distinct weaver colony or roosting site, separated from each other by at least 300 m. So although movement recorded going into and out of these sites may not strictly constitute “dispersal”, I assumed that the features of the sites and the matrix surrounding them would influence these movements in much the same way as they would affect true immigrations and emigrations. My study was therefore a finer scale examination of movements into and out of sites, rather than patches.

3. Determining the movement into and out of each site (response variable)

The response variable in this study was the amount of weaver movement into and out of each site. The raw data from SAFRING included one record for each time a bird was captured. Each record held the unique ring number, the date and location of capture and the species details. In R (version 3.0.2, R Development Core Team, 2013) I identified unique ring numbers and created a “recapture” dataset that consisted of only those records of birds that were captured more than once. I then wrote a “for loop” in R to create an “edge list” from the recapture dataset which had three columns: “ring number”, “site from” and “site to” and each row in the edge list referred to a bird movement from one site to another. Many of these movements were actually recaptures within the same site so to remove these “non-movements” I calculated the Great Circle (geographic) distances between all the sites using the “*fields*” package (Fields Development Team 2006) in R. I then assigned these distances to the appropriate movements in the edge list and removed all movements with a distance of 0 km. I converted this list into a 42 by 42 matrix that showed the number of movements from each site (rows) into each site (columns). By summing the columns and rows of this matrix I obtained the total number of movements coming into and going out of each of the sites.

The high variation in sampling effort between sites would probably have had a strong influence on the detection of weaver movement coming into and out of the sites. A site that had been sampled extensively would have had more weavers caught and ringed at it, improving the chances of a weaver being detected moving out of the site (when they are caught somewhere else) and/or moving into the site (when weavers from other sites are caught there). Whereas, detecting movement into and out of a site that received less effort would be less likely. Sampling effort therefore needed to be controlled for. Net hours (length of mist nets x hours mist nets were open) were recorded for most of the sites, but some did not have a measure of effort. However, all the sites had a value for the total number of birds caught in mist nets over the entire sampling period. For all the sites that did have effort data, a significant and positive relationship was found between net hours (log) and number of birds caught (log) (corr = 0.91, t_{51} = 15.72, p < 0.001) (Fig. 2). Thus, the number of birds caught was used as a proxy for effort and the amount of movement into and out of each site was divided by this proxy. The response variable for the analyses was therefore the amount of movement into and out of the sites, controlled for effort.

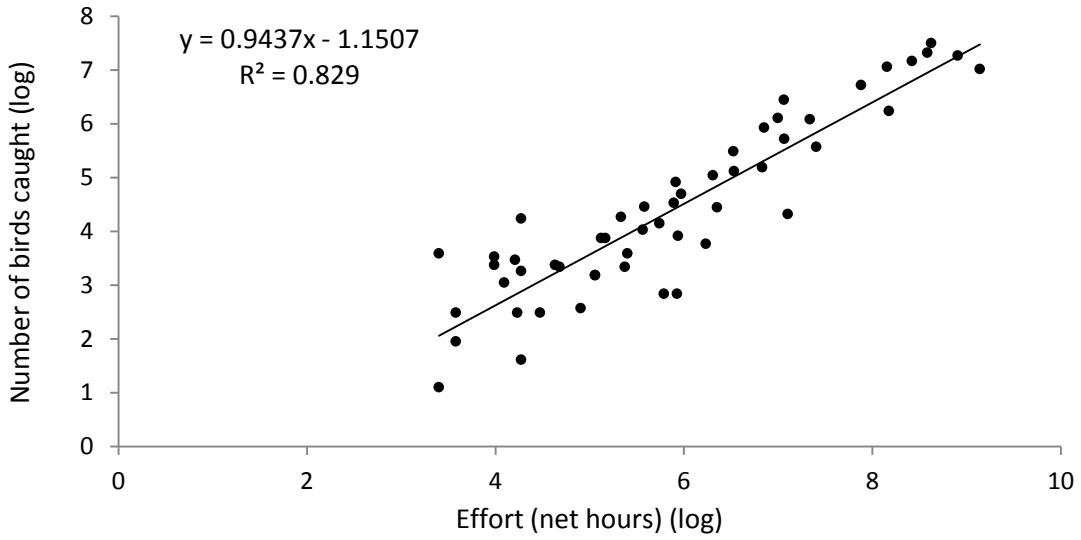

Figure 2. Correlation between the amount of sampling effort (net hours) (log) and the number of birds caught in the nets (log) at each of the sites that had effort data (n = 53) (prior to collapsing sites to the final 42). There was a strong, positive and significant relationship between the two variables (corr = 0.91, t_{51} = 15.72 p < 0.001).

4. *Predictor variables*

4.1 Proximity measures

Movement into and out of a site could be influenced by how close a site is to the other sites (Bowler & Benton 2005). I calculated three increasingly complex measures of proximity for each site: nearest neighbour (NN), the "Turner" proximity index (proximity_Turner) and the "Esselstyn" proximity index (proximity_Esselstyn).

Nearest neighbour distance is simply the distance from a site to its closest neighbour (Fahrig 2003) and I computed this value for each site in R using the *fields* package.

The "Turner" proximity index (proximity_Turner) was calculated for each site using the following equation (Turner et al. 2001):

$$Proximity\_Turner_i = \sum \frac{S_k}{n_k}$$

where S_k is the size of a neighbouring wetland and n_k is the distance from the focal site *i* to site *k.* High values of this index indicate that a site is relatively well connected to other sites, whereas a low value indicates that a site is relatively isolated from other sites. The areas of the wetlands associated with each site were measured in ArcMap 10 (ESRI 2011) using a wetland layer and aerial photographs (taken in 2010) obtained from the National Geo-spatial Information centre (NGI, see: http://www.ngi.gov.za). I used the *fields* package in R to calculate the distances between sites and computed the "Turner" proximity index.

The "Esselstyn" proximity index (proximity_Esselstyn) is adapted from a proximity index used by Esselstyn et al. (2004) which does not take into account the area of neighbouring habitat patches. This index was calculated in R using the following equation:

$$Proximity\_Esselstyn_i = \frac{\sum_{i=1}^{n} (1/D^2)}{n-1}$$

where *D* is the distance from the focal site *i* and *n* is the number of sites (42). As with the Turner proximity index, high values indicate relatively high connectivity whereas low values indicate that a site is relatively isolated.

4.2 Site Variables:

4.2.1 Wetland size

Patch size may influence the movement of animals into and out of a site (Bowler & Benton 2005) so it was important to include the size of the wetland as a site variable. The size of the wetland that a site was associated with was measured in ArcGIS 10 and included as a site variable.

4.2.2 Field work: point counts

Bird movement to and from a site can be strongly influenced by the features of the site itself (Bowler & Benton 2005). This study did not allow time for vegetation sampling; however bird populations can act as decent indicators of habitat quality (Johnson 2007) so a measure of bird abundance at each site could potentially be a proxy for site quality. As colonial species (Hockey et al. 2005), weaver movement might also be affected by the presence of conspecifics (Bowler & Benton 2005) so an indication of the number of weavers at each site was an important confounding variable to include in the analysis.

To acquire an estimate of the bird abundance and weaver colony size at each site, I conducted one thirty-minute, early morning bird count at each site during November 2013. These counts were preceded by a ten minute habituation period to allow birds to become accustomed to our presence. November falls within Cape Town's summer and is a good time of year for bird counts as many residents are breeding and many migrants are visiting (Hockey et al. 2005). The bird counts were conducted between 6 am and 9 am on clear mornings and involved counting all birds within a 150 m radius of the mist netting site. I was accompanied by the same experienced field assistant on every count to ensure consistency in sighting effort. These counts provided two values for each of

the 42 sites that I used in the analyses: total number of birds counted, and the total number of weavers counted.

4.3 Matrix variables and river length

The focal question of this study asked how weaver movement was influenced by the nature of the matrix surrounding the wetland sites. ArcGIS 10 was used to extract information on land cover from around the sites. The 42 sites were plotted using the Transverse Mercator projection, because it is a good "general purpose" projection as it preserves areas, distances and directions over a small area (less than two degrees of longitude wide). It was therefore an appropriate projection to use in my study as I focused on just the Cape Town area.

As in all aspects of landscape ecology, it is important to study the urban system at the appropriate spatial scale (Savard et al. 2000). When unsure of the scale at which to study the species' response to the landscape, it can be useful to employ a multi-scale approach in which one investigates the species response to the landscape at a number of scales (Dunford & Freemark 2005; Bergman et al. 2012; Meffert & Dziock 2013). In this study I investigated the possible influence of the urban matrix on weaver movement at three spatial scales by extracting land cover information from buffers of varying radii around each site.

Firstly, a buffer size of 400 m was drawn around the sites as this roughly relates to the dispersal distance of weaver birds in this study. In an evaluation of patch connectivity measures, Prugh (2009) set the radius of buffers around habitat patches to $1/\alpha$ (the average migration distance of each study species), the best performing decider of buffer radius according to Moilanen and Nieminen (2002). The average distance travelled by weavers in this study (excluding "non-movements") was 2.37 km so the buffer radius was chosen to be 400 m as 1 / 2.37 km = 0.422 km = 422 m. To detect any response to the urban matrix at an immediate scale, I drew buffers with a

radius of 100 m around each site. Lastly, the largest buffer radius was set at 1000 m to distinguish a response at a broader spatial scale.

I obtained the area of each land class falling in each of the three buffers around all 42 sites from a detailed land cover map obtained from the Council for Scientific and Industrial Research (CSIR; see http://www.csir.co.za). The classes in the land cover raster were classified at a finer scale than was necessary for this study so I grouped them into five broad land cover groups: urban industrial, urban residential, natural vegetation, planted vegetation, and water bodies. I also projected a detailed river layer obtained from the NGI and extracted the length of river in each of the three buffers around all 42 sites. River length was included as a matrix variable to detect if rivers were used as movement corridors at different scales.

5. Statistical analysis

The main challenge in analysing these data, and in addressing the research questions, was to include all necessary variables without over parameterizing the models. Because the sample size was 42, I aimed to reduce the number of variables to around seven.

5.1 Reducing the matrix variables

For each scale (100 m, 400 m, and 1000 m buffer radii) there were essentially six variables; five proportions of each land use types as well as river length in metres. I used principal components analysis (PCA) with a varimax rotation in R to reduce the five land use proportions at each scale to a limited number of independent variables that could then be used as predictors in further analyses. When using PCA to reduce the number of variables, it is preferable that there are linear relationships between the variables so I arcsine square root transformed the variables as they were proportions (Quinn & Keough 2002). For each scale, I retained the principle components that cumulatively explained at least 70% of the variation and had eigenvalues greater than one (Quinn & Keough

2002). I used the scores for these three components as well as river length at each scale as the new "buffer variables" at each scale.

5.2 Analysis procedure

The majority of the analysis procedure was performed in PRIMER-E (Clarke & Gorley 2006) with the add-on package PERMANOVA+ (Anderson et al. 2008). The analyses were carried out on movement into and out of sites both overall (multivariate response) and separately (univariate responses). I used distance-based linear models (DISTLMs) in PERMANOVA+ to investigate relationships between the response and predictor variables. DISTLM is a non-parametric, multivariate multiple regression technique for analysing and modelling the relationship between one or more response variable (as described by a resemblance matrix) and sets of predictor variables (Anderson et al. 2008). DISTLMs can be used to partition the variation in the response variable explained by groups of predictor variables (Anderson et al. 2008). DISTLM is a permutation-based technique that does not make the assumption of normality associated with standard linear modelling approaches, and is thus appropriate for ecological data that often fails to meet these assumptions (Anderson et al. 2008). However, it is preferable that the variables are not heavily skewed so I transformed the response and predictor variables using $\log_{10}$, square root and fourth root transformations where necessary to improve linearity. I also standardized all the variables so that they were all on the same scale by subtracting the mean then dividing by the standard deviation and then added 10 to ensure no negative values. DISTLMs require the response variable to be described as a resemblance matrix (Anderson et al. 2008). There are no hard and fast rules pertaining to the type of dissimilarity measure used to create resemblance matrices especially for the rather unique response variable used in this study. I used Euclidean distance as this is often used when the response variable is an index (movement controlled for effort) and is used when the response is univariate (the response variable in my analyses were sometimes univariate) (Anderson et al. 2008). When Euclidean distance is used as the basis of a model, DISTLM will fit a traditional

model of predictor variables and response variables and produces *F* and R^2 statistics equivalent to those produced by a multiple linear regression (Anderson et al. 2008). All DISTLMs were run with 9999 permutations and all the models used the AICc selection criteria. AICc is an appropriate selection criterion when the response is univariate and when the ratio of sample size (n) to number of variables (V) is high (N/V < 40) (Anderson et al. 2008). So in a situation where sample size is 42, it is appropriate to use AICc.

After creating the Euclidean distance matrix I ran the following procedure on each response variable(s) (represented by a resemblance matrix):

1. *Accounting for spatial autocorrelation:*

   Ecological patterns can often be explained by the geographical positioning of study sites (Borcard et al. 1992) so to address the possibility of spatial autocorrelation in the response variable I produced 15 spatial interaction terms for each site up to the third order based on the geographic co-ordinates of each site (e.g. x, y, x^2, y^2, x^3, y, x^2y, xy^2, x^2y, etc...,up to x^3y^3), following Dures and Cumming (2010). I ran separate DISTLMs testing for any relationships between the interaction terms and the response variable and if any were found to be significant ($\alpha = 0.05$), they would be included in further analyses.

2. *Confounding variables:*

   The mist net sampling was conducted inconsistently at each site. Some sites were mist netted regularly over many years, some were visited sporadically over fewer years, and others were visited just a couple of times in total. To account for this temporal variation in sampling effort, I included the average of all the sampling dates at each site and the standard deviation of these dates (in number format) as confounding variables. I ran a stepwise DISTLM to determine which confounding variables, if any, had a significant influence on the response. The stepwise selection reaches the final model by first adding the term that explains the most variation, then seeks to add one that will improve the selection

criteria (lower the AICc score) and continues in this way until the most parsimonious model is decided upon, but at each step the model also attempts to improve the selection criteria by potentially removing a variable. This procedure stops when no further improvements can be made by including or removing another term (Anderson et al. 2008). The confounding variable(s) would be including in further analyses if found to be significant (α = 0.05) in the stepwise DISTLM.

When investigating the effect that effort may have on movement when not already controlled for in the response, the proxy for effort (total number of birds caught at a site) was included in this step of the procedure as an additional confounding variable.

3. *Proximity variables:*

   Draftsman's plots of the three proximity variables (NN, proximity_Turner, and proximity_Esselstyn) were created in PRIMER-E to look for possible multi-collinearity and to avoid including redundant variables in the final models. I ran a stepwise DISTLM to decide which of these variables should be included in the final model. A proximity index was included in further analyses if found to be significant (α = 0.05) in the stepwise DISTLM.

4. *Grouped final model:*

   To investigate the influence that subsequent groups of variables had on the response, I ran "all selected" DISTLMs with the groups of variables included in the model in a specified order of: spatial (if any), confounding (if any), proximity (if any), site variables and then buffer variables (at one scale for each model). This would allow me to explicitly examine the proportion of variation explained by a particular set of variables (e.g. buffer) over and above the variation explained by previous group(s) (e.g. proximity and site) (Anderson et al. 2008). This technique also produces "marginal tests" which test the relationships between the groups of variables and the response separately but do correct for multiple testing (Anderson et al. 2008).

5. *Relative important of individual variables*

I ran step-wise DISTLMs to explore the correlations between individual predictor variables (not grouped) and the response variables and to see which variables were included in the most parsimonious model. Because of certain logical and statistical flaws associated with stepwise selection, Quinn and Keough (2002) suggested that other, comparatively parsimonious models should also be considered. To cross validate the selection of variables in the stepwise DISTLMs, I ran a DISTLM that used the "best" selection procedure on all possible combinations of the variables (ungrouped at each scale) to produce a set of top models based on AICc scores. Models that are within 2 AICc units of the most parsimonious model can be considered as potential "best" models and the variables present in these models should be considered as potential predictors (Burnham & Anderson 2002; Quinn & Keough 2002).

This analysis procedure was carried out with the following response variables: overall movement (in and out), movement into sites, and movement out of sites. It was also carried out to test the relative influence of effort as a confounding variable when it is not controlled for in the response.

Results

The movement dataset contained 7862 entries from 6591 individual birds which relates to 1271 recapture records. The recapture records were from 1033 individual birds. Most of these recaptures represented movement within the same site and only 453 represented movement between sites. Most of the sites had some movement into or out of them but eight did not have any movement at all.

Accounting for spatial autocorrelation and confounding temporal variables

The analysis used to address the issue of spatial autocorrelation (adapted from Borcard et al. (1992)) revealed that none of the spatial interaction terms had a significant influence on any of the response variables (Table 1) so they were not included in any subsequent tests. Likewise, the confounding variables relating to sampling dates (average and standard deviation) were found to be non-significant predictors in the stepwise DISTLMs for all three response variables and were therefore not included in further analyses (Table 2).

Table 1. Marginal test statistics from distance-based linear models (DISTLMs) testing for correlations between 15 spatial interaction terms and four response variables (represented as resemblance matrices): overall movement not controlled for effort, and overall movement, movement in and movement out of sites all controlled for effort. SS is the sum of squares, *F* is the pseudo-F statistic and p_{perm} is the p-value for each marginal test. Each marginal test had 40 degrees of freedom.

	Not controlled for effort			Controlled for effort								
	Overall movement			Overall Movement			Movement out			Movement in		
Variable	SS	*F*	p_{perm}	SS	*F*	p_{perm}	SS	*F*	p_{perm}	SS	*F*	p_{perm}
x	1.55	0.77	0.40	1.34	0.66	0.47	0.73	0.72	0.41	0.61	0.60	0.39
y	2.73	1.38	0.24	1.74	0.87	0.42	0.04	0.04	0.84	1.70	1.73	0.20
x^2	1.56	0.78	0.41	1.35	0.67	0.47	0.73	0.73	0.40	0.62	0.61	0.38
y^2	2.73	1.38	0.24	1.74	0.87	0.43	0.04	0.04	0.85	1.70	1.73	0.20
x^3	1.57	0.78	0.41	1.36	0.68	0.47	0.74	0.74	0.39	0.62	0.62	0.39
y^3	2.72	1.37	0.24	1.74	0.86	0.42	0.04	0.04	0.84	1.70	1.73	0.20
xy	0.57	0.28	0.66	1.33	0.66	0.52	0.85	0.85	0.36	0.47	0.47	0.52
xy^2	1.71	0.85	0.36	1.59	0.79	0.46	0.37	0.37	0.55	1.21	1.22	0.28
xy^3	2.13	1.06	0.31	1.66	0.83	0.44	0.22	0.22	0.65	1.43	1.45	0.23
x^2y	0.19	0.09	0.86	1.15	0.57	0.54	1.15	1.15	0.29	0.00	0.00	0.99
x^2y^2	0.57	0.28	0.66	1.33	0.66	0.53	0.86	0.85	0.36	0.47	0.46	0.52
x^2y^3	1.27	0.63	0.44	1.50	0.74	0.48	0.55	0.54	0.48	0.95	0.95	0.35
x^3y	0.50	0.25	0.69	1.18	0.58	0.52	1.10	1.10	0.31	0.08	0.08	0.75
x^3y^2	0.16	0.08	0.88	1.19	0.59	0.55	1.10	1.11	0.29	0.08	0.08	0.77
x^3y^3	0.56	0.28	0.67	1.33	0.66	0.53	0.86	0.86	0.36	0.47	0.46	0.51

Table 2. Test statistics for stepwise distance-based linear models (DISTLMs) (AICc selection criteria) showing which confounding variable was included in the sequential test and whether the inclusion was significant. Response variables were: overall movement not controlled for effort, and overall movement, movement in and movement out of sites all controlled for effort. Confounding variables were average sampling date (log), standard deviation of sampling date, and effort (total count (log))was a third confounding variable in the first model. "SS" is the sum of squares, *F* is the pseudo-F statistic, p_{perm} is the p-value and "Var. (%)" is the percentage of variation explained. Asterisks indicate predictors explaining a significant proportion of variation in the response variable ($\alpha = 0.05$).

Variable	AICc	SS	*F*	p_{perm}	Var (%)	Residual df
Overall movement not controlled for effort						
TotalCount_log	-1.9128	45.78	50.56	0.0001*	55.83	40
Overall movement, controlled for effort						
StdDevDate	30.159	4.27	2.20	0.1113	5.21	40
Movement in, controlled for effort						
StdDevDate	1.0174	2.16	2.23	0.148	5.28	40
Movement out, controlled for effort						
AverageDate_log	0.48728	2.65	2.77	0.105	6.47	40

Selecting a proximity variable

A draftsman's plot revealed that the nearest neighbour (NN) distance and the "Esselstyn" proximity index were highly correlated (R = -0.86) so NN was excluded from further analyses. The stepwise DISTLMs on the two remaining proximity indices included only the "Esselstyn" proximity index in the final models, indicating that it alone was a sufficient predictor, and thus only proximity variable to be included in further analyses (Table 3).

Table 3. Test statistics for stepwise distance-based linear models (DISTLMs) (AICc selection criteria) showing which proximity index was included in the sequential test and whether the inclusion was significant. Response variables were: overall movement not controlled for effort, and overall movement, movement in and movement out of sites all controlled for effort. Proximity variables were "Turner" proximity index (log) and "Esselstyn" proximity index (square root). "SS" is the sum of squares, *F* is the pseudo-F statistic, p_{perm} is the p-value and "Var. (%)" is the percentage of variation explained. Asterisks indicate predictors explaining a significant proportion of variation in the response variable ($\alpha = 0.05$).

Variable	AICc	SS	*F*	p_{perm}	Var (%)	Residual df
Overall movement not controlled for effort						
Prox_Esselstyn_sqrt	22.794	16.78	10.29	0.002*	20.46	40
Overall movement, controlled for effort						
Prox_Esselstyn_sqrt	15.179	27.59	20.29	0.0001*	33.65	40
Movement in, controlled for effort						
Prox_Esselstyn_sqrt	-12.519	12.86	18.29	0.0001*	31.38	40
Movement out, controlled for effort						
Prox_Esselstyn_sqrt	-15.398	14.73	22.43	0.0002*	35.92	40

Without controlling for effort prior to analysis

To test whether effort was an important factor to account for in the response, I ran the DISTLM analysis procedure without first controlling for effort and instead included it as a confounding variable. The stepwise DISTLM run with the confounding variables (effort, average sampling date and SD sampling date) showed that effort (Total count (log)) was the only variable to have a significant influence on the variation explained ($F_{1,40} = 50.56$, $p_{perm} = 0.0001$)(Table 2) so was therefore the only confounding variable included in the final model. When effort was not controlled for in the response variable and rather included as a confounding variable, it explained a significant 55.83% of the total variation ($F_{1,40} = 50.56$, $p_{perm} = 0.0001$)(Table 4). The sequential tests showed that once the variation explained by effort was accounted for, the proximity index explained a further, significant 21.03% of the remaining variation ($F_{1,40} = 35.43$, $p_{perm} = 0.0001$)(Table 4). None of the sequential tests showed a significant improvement in the variation explained with addition of the site or buffer variables (Table 4). Not only did the proxy for effort have an overwhelmingly significant influence in the model, but adding it as a further variable increased the risk of over

parameterization, supporting my decision to correct for it in the response variable rather than treat it as an independent variable.

Table 4. Test statistics of distance-based linear models (DISTLMs) investigating the relationships between the overall movement into and out of wetland sites (not controlled for effort) and sets of predictor variables. The marginal tests show the individual relationships between the group of predictor variables and the response. The sequential tests show the cumulative variation explained by each set of predictor variables and were performed using the "all-selected" selection procedure and AICc selection criteria. See methods for description of variable groups. "SS" is the sum of squares, *F* is the pseudo-F statistic, p_{perm} is the p-value, "Var. (%)" is the percentage of variation explained and "Cum. var. (%)" is the cumulative percentage of variation explained. Asterisks indicate predictors explaining a significant proportion of variation in the response variable ($\alpha = 0.05$).

Variable Group	AICc	SS	*F*	p_{perm}	Var (%)	Cum. Var (%)	Residual df
Marginal tests							
Effort	-	45.78	50.56	0.0001*	55.83	-	40
Proximity	-	16.78	10.29	0.0024*	20.46	-	40
Site	-	7.70	1.31	0.2783	9.40	-	38
Buffer 100	-	4.69	0.56	0.7237	5.72	-	37
Buffer 400	-	2.52	0.29	0.9243	3.08	-	37
Buffer 1000	-	4.82	0.58	0.7070	5.87	-	37
Sequential tests for 100 m buffer							
Effort	-1.9128	45.78	50.56	0.0001*	55.83	55.83	40
+ Proximity	-26.734	17.24	35.43	0.0001*	21.03	76.86	39
+ Site	-22.583	1.57	1.08	0.3838	1.91	78.77	36
+ Buffer 100	-10.899	0.41	0.20	0.9902	0.51	79.27	32
Sequential tests for 400 m buffer							
Effort	-1.9128	45.78	50.56	0.0001*	55.83	55.83	40
+ Proximity	-26.734	17.24	35.43	0.0001*	21.03	76.86	39
+ Site	-22.583	1.57	1.08	0.3835	1.91	78.77	36
+ Buffer 400	-11.151	0.52	0.24	0.9802	0.63	79.40	32
Sequential tests for 1000 m buffer							
Effort	-1.9128	45.78	50.56	0.0001*	55.83	55.83	40
+ Proximity	-26.734	17.24	35.43	0.0001*	21.03	76.86	39
+ Site	-22.583	1.57	1.08	0.3793	1.91	78.77	36
+ Buffer 1000	-14.319	1.74	0.89	0.5199	2.13	80.89	32

Influence of grouped proximity, site and buffer variables on overall movement

Table 5 summarises the results of the DISTLM analyses that tested the relationships between the sets of predictor variables and the overall movement at the sites. The marginal tests showed that proximity was the only predictor variable that alone had a significant effect on overall movement (explained 33.65%, $F_{1,40}$ = 20.29, p_{perm} = 0.0001)(Table 5). Once the variation explained by proximity was accounted for, the site variables explained a further 10.31% of the variation and this contribution was borderline not significant ($F_{1,38}$ = 2.27, p_{perm} = 0.0576). The grouped buffer variables measured at the 100 m scale did not significantly contribute to the variation explained (explained = 1.14%, $F_{1,33}$ = 0.17, p_{perm} = 0.995), nor did those at the 400 m scale (explained = 3.69 , $F_{1,33}$ = 0.58, p_{perm} = 0.8002) or at the 1000 m scale (explained = 4.73%, $F_{1,33}$ = 3.88, p_{perm} = 0.6308)(Table 5). The model with the lowest AICc value was that which included both proximity and site variables (Table 5) suggesting that although the addition of the site variables may not have been strictly significant, it may have improved parsimony. The addition of the buffer variables (at all scales) resulted in a large increase in the AICc values indicating a reduction in parsimony (Table 5).

Table 5. Test statistics of distance-based linear models (DISTLMs) investigating the relationships between the overall movement into and out of wetland sites (once controlled for effort) and sets of predictor variables. The marginal tests show the individual relationships between the group of predictor variables and the response. The sequential test show the cumulative variation explained by each set of predictor variables and were performed using the "all-selected" selection procedure and AICc selection criteria. See methods for description of variable groups. "SS" is the sum of squares, *F* is the pseudo-F statistic, p_{perm} is the p-value, "Var. (%)" is the percentage of variation explained and "Cum. var. (%)" is the cumulative percentage of variation explained. Asterisks indicate predictors explaining a significant proportion of variation in the response variable ($\alpha = 0.05$).

Variable Group	AICc	SS	*F*	p_{perm}	Var (%)	Cum. Var (%)	Residual df
Marginal tests							
Proximity	-	27.59	20.29	0.0001*	33.65	-	40
Site	-	6.42	1.08	0.3855	7.83	-	38
Buffer 100	-	7.55	0.94	0.4978	9.20	-	37
Buffer 400	-	4.19	0.50	0.8499	5.11	-	37
Buffer 1000	-	12.35	1.64	0.1224	15.06	-	37
Sequential tests for 100 m buffer							
Proximity	15.179	27.59	20.29	0.0001*	33.65	33.65	39
+ Site	15.443	8.46	2.27	0.0576	10.31	43.96	37
+ Buffer 100	26.538	0.93	0.17	0.995	1.14	45.10	33
Sequential tests for 400 m buffer							
Proximity	15.179	27.59	20.29	0.0001*	33.65	33.65	39
+ Site	15.443	8.46	2.27	0.0576	10.31	43.96	37
+ Buffer 400	24.538	3.03	0.58	0.8002	3.69	47.66	33
Sequential tests for 1000 m buffer							
+ Proximity	15.179	27.59	20.29	0.0001*	33.65	33.65	39
+ Site	15.443	8.46	2.27	0.0576	10.31	43.96	37
+ Buffer 1000	23.700	3.88	0.76	0.6308	4.73	48.69	33

Influence of grouped proximity, site and buffer variables on movement into and movement out of sites

The same analysis procedure was carried out on the movement into sites and movement out of sites separately to see if the predictor variable groups influenced these two measures of movement differently (Tables 6 and 7). Much like the analysis on overall movement, the sequential

tests showed that once the 31.38% of the variation explained by proximity was accounted for ($F_{1,40}$ = 18.29, p_{perm} = 0.0001), the site variables had a borderline not significant effect on movement into the sites (explained 13.38%, $F_{1,38}$ = 2.99, p_{perm} = 0.0531)(Table 6). The addition of site variables in the "movement in" model resulted in a lower AICc value and higher cumulative proportion of variation explained (Table 6) indicating that these variables might improve the explanatory power of the model whilst improving parsimony. On the other hand, once the 34.92 % explained by proximity was accounted for ($F_{1,38}$ = 22.43, p_{perm} = 0.0001), site variables did not contribute significantly to the variation of movement out of sites ($F_{1,38}$ = 0.63, p_{perm} = 0.5978) and the addition of site variables reduced the parsimony (Table 7). Once the variation explained by proximity and site variables was accounted for, none of the buffer variable groups had a significant influence on movement in or out of the sites and adding the buffer variables (at all scales) reduced the parsimony in every model indicated by the larger AICc values (Table 6 and 7).

Table 6. Test statistics of distance-based linear models (DISTLMs investigating the relationships between the movement into wetland sites (once controlled for effort) and sets of predictor variables. The marginal tests show the individual relationships between the group of predictor variables and the response. The sequential test show the cumulative variation explained by each set of predictor variables and were performed using the "all-selected" selection procedure and AICc selection criteria. See methods for description of variable groups. "SS" is the sum of squares, *F* is the pseudo-F statistic, p_{perm}, is the p-value, "Var. (%)" is the percentage of variation explained and "Cum. var. (%)" is the cumulative percentage of variation explained. Asterisks indicate predictors explaining a significant proportion of variation in the response variable (α = 0.05).

Variable Group	AICc	SS	*F*	p_{perm}	Var (%)	Cum. Var (%)	Residual df
Marginal tests							
Proximity	-	12.86	18.29	0.0001*	31.38	-	40
Site	-	4.47	1.55	0.2162	10.90	-	38
Buffer 100	-	3.29	0.81	0.5326	8.01	-	37
Buffer 400	-	1.81	0.43	0.7912	4.41	-	37
Buffer 1000	-	5.45	1.42	0.246	13.30	-	37
Sequential tests for 100 m buffer							
Proximity	-12.519	12.86	18.29	0.0001	31.38	31.38	40
+ Site	-14.266	5.48	2.99	0.0531	13.38	44.75	37
+ Buffer 100	-2.8304	0.28	0.10	0.9824	0.68	45.44	33
Sequential tests for 400 m buffer							
Proximity	-12.519	12.86	18.29	0.0001	31.38	31.38	40
+ Site	-14.266	5.48	2.99	0.0531	13.38	44.75	37
+ Buffer 400	-4.5995	1.20	0.46	0.7667	2.93	47.69	33
Sequential tests for 1000 m buffer							
Proximity	-12.519	12.86	18.29	0.0002	31.38	31.38	40
+ Site	-14.266	5.48	2.99	0.0531	13.38	44.75	37
+ Buffer 1000	-3.9316	0.86	0.33	0.8515	2.10	46.85	33

Table 7. Test statistics of distance-based linear models (DISTLMs) investigating the relationships between the movement out of wetland sites (once controlled for effort) and sets of predictor variables. The marginal tests show the individual relationships between the group of predictor variables and the response. The sequential tests show the cumulative variation explained by each set of predictor variables and were performed using the "all-selected" selection procedure and AICc selection criteria. See methods for description of variable groups. "SS" is the sum of squares, *F* is the pseudo-F statistic, p_{perm}, is the p-value, "Var. (%)" is the percentage of variation explained and "Cum. var. (%)" is the cumulative percentage of variation explained. Asterisks indicate predictors explaining a significant proportion of variation in the response variable ($\alpha = 0.05$).

Variable Group	AICc	SS	*F*	p_{perm}	Var (%)	Cum. Var (%)	Residual df
Marginal tests							
Proximity	-	14.73	22.43	0.0001*	35.92	-	40
Site	-	1.95	0.63	0.5978	4.77	-	38
Buffer 100	-	4.26	1.07	0.384	10.39	-	37
Buffer 400	-	2.38	0.57	0.6831	5.81	-	37
Buffer 1000	-	6.89	1.87	0.138	16.81	-	37
Sequential tests for 100 m buffer							
Proximity	-15.398	14.73	22.43	0.0001*	35.92	35.92	40
+ Site	-13.081	2.97	1.57	0.2081	7.25	43.17	37
+ Buffer 100	-2.3191	0.65	0.24	0.9145	1.60	44.77	33
Sequential tests for 400 m buffer							
Proximity	-15.398	14.73	22.43	0.0001*	35.92	35.92	40
+ Site	-13.081	2.97	1.57	0.2081	7.25	43.17	37
+ Buffer 400	-4.5492	1.83	0.70	0.5894	4.45	47.62	33
Sequential tests for 1000 m buffer							
Proximity	-15.398	14.73	22.43	0.0001*	35.92	35.92	40
+ Site	-13.081	2.97	1.57	0.2081	7.25	43.17	37
+ Buffer 1000	-6.9466	3.02	1.23	0.3282	7.36	50.53	33

Relative important of individual variables (Stepwise and "best" models)

Tables 8, 9 and 10 summarise the results from the stepwise DISTLMs that investigated the correlations between each individual predictor variable and the three response variables (overall movement, movement in and movement out). The stepwise selection criteria arrived at the single most parsimonious model, but models within two AICc units of the most parsimonious model should

also be considered (Burnham & Anderson 2002; Quinn & Keough 2002). Appendices 1, 2 and 3 present each of the sets of "best" models explaining overall movement, movement in and movement out respectively. The most parsimonious models selected by the stepwise procedure had the same variable combination as the most parsimonious models selected by the "best" selection procedure because both methods used AICc selection criteria. Figure 3 summarises how frequently each predictor variable appears in the sets of best models for overall movement (in and out) and for movement in and movement out separately (run at the three scales) as a percentage of the number of best models.

The strong influence of proximity is clear in the stepwise DISTLMs as it is consistently significant in the marginal tests and is always the first variable selected in the sequential tests (Table 8, 9 and 10). Proximity was present in 100% of all the sets of best models for both movement in and movement out at all three scales (Fig. 3). Pearson's correlations showed that proximity had significant, positive relationships with both the movement into sites (corr = 0.56, t_{40} = 4.28, p < 0.0001) and out of the sites (corr = 0.60, t_{40} = 4.74, p < 0.0001)

The size of the wetlands (WetlandSize_log) did not have a significant effect in the marginal tests (Tables 8, 9 and 10), was not included in the stepwise model selection, and did not appear in more than 40% of any of the sets of best models (Fig. 3) indicating that is unlikely to have been a major contributor to the variation explained. There did not seem to be a difference in the presence of this variable in the "movement in" and "movement out" sets of models (Fig. 3).

The number of weavers counted at the sites in 2013 (WeaverCount2013) was included in the stepwise selected model explaining movement into the sites and this inclusion was significant ($F_{1,39}$ = 4.67, p_{perm} = 0.0388). This variable appeared in between 63 and 67% of the best models explaining movement into sites (at all the scales) (Fig. 3). On the other hand, this variable was not included in the stepwise selected models explaining movement out of sites and was absent from all the "movement out" best models at all scales (Fig. 3).

The total number of birds counted at the sites in 2013 (BirdCount_sqrt) was included in the stepwise selected models for overall movement (Table 8), movement in (Table 9) and movement out (Table 10). The inclusion of this variable in the overall movement model was significant ($F_{1,39}$ = 3.56, p_{perm} = 0.0388)(Table 8), but was not significant in the "movement in" model ($F_{1,39}$ = 3.12, p_{perm} = 0.0827) (Table 9) nor in the "movement out" model ($F_{1,39}$ = 3.02, p_{perm} = 0.0889)(Table 10). This variable was present in between 50 and 83% of the best models in each set (Fig. 3), suggesting that although it did not always have a strictly significant effect in the stepwise models, may be an important variable to consider.

At the 100 m scale, none of the variables representing land use (PC1_100, PC2_100, PC3_100) were included in any of the stepwise models (Tables 8, 9 and 10) nor did they appear in any of the three sets of best models (Fig. 3). At the 400 m scale, PC2_400 was included in the stepwise selected model explaining movement out of the sites but this inclusion was not significant ($F_{1,39}$ = 3.40, p_{perm} = 0.0716). This variable appeared in 57% of the best models explaining movement out of sites, suggesting that although it did not have a strictly significant effect in the stepwise model, may still be a variable worth considering in terms of explaining movement out of sites. This PC represents gradients in the proportion of industrial urban area at this scale and the proportion of wetland habitat at this scale (Table 11). PC3_400 appeared in 14% of the best models explaining movement out, and this variable represents gradients in the proportions of planted vegetation and wetland area around the site at this scale (Table 11). None of the 400 m matrix variables appeared in any of the models explaining movement into the sites (Fig. 3).

At the 1000m scale, PC2_1000 showed a significant effect in the marginal test investigating the effects of predictor variables on movement out of sites ($F_{1,40}$ = 4.63, p_{perm} = 0.0361) but was not included in the sequential test (Table 10) and was only present in one of the best models explaining movement out of sites (Fig. 3), suggesting that it was unlikely to have had a large effect on movement out of sites. Although PC1_1000 was not included in the stepwise-selected models, it

appeared in 50% of the best models explaining movement out of sites and in 25% of the best models explaining movement into sites (Fig. 3), suggesting that this variable may have had an influence on movement. This PC1_1000 component represents gradients in the proportions of residential urban area and wetland area at this scale (Table 11).

Regardless of the scale at which it was measured, river length (m) did not have a significant effect on any of the response variables and was not included in any of the stepwise models (Tables 8, 9 and 10); however, it was present in some of the "best" models (Fig. 3). At 100 m, river length appeared in a third of the best models explaining movement into the sites and in a third of the best models explaining movement out of the sites (Fig. 3). At the 400 m scale, river length appeared in 38% of the best models explaining movement into the sites and in 14% of the best models explaining movement out of the sites (Fig. 3). And at the 1000 m scale, river length appeared in 13% of the "movement in" models and in 40% of the "movement out" models (Fig. 3).

Table 8. Test statistics of distance-based linear models (DISTLMs) investigating the relationships between the overall movement in and out of wetland sites (once controlled for effort) and the individual predictor variables. The marginal tests show the individual relationships between the predictor variables and the response. The sequential tests show the variables selected by the stepwise selection procedure based on AICc selection criteria. "SS" is the sum of squares, *F* is the pseudo-F statistic, p_{perm}, is the p-value, "Var. (%)" is the percentage of variation explained and "Cum. var. (%)" is the cumulative percentage of variation explained. Asterisks indicate predictors explaining a significant proportion of variation in the response variable (α = 0.05).

Variable Group	AICc	SS	*F*	p_{perm}	Var (%)	Cum. Var (%)	Residual df
Marginal tests							
Prox_Essel_sqrt	-	27.59	20.29	0.0001*	33.65	-	40
WetlandSize_log	-	0.12	0.06	0.9482	0.15	-	40
WeaverCount2013	-	2.60	1.31	0.2604	3.17	-	40
BirdCount_sqrt	-	4.54	2.35	0.1085	5.54	-	40
PC1_100	-	1.86	0.93	0.4061	2.26	-	40
PC2_100	-	0.80	0.39	0.6415	0.97	-	40
PC3_100	-	2.41	1.21	0.3127	2.93	-	40
River100_sqrt	-	0.72	0.35	0.7349	0.88	-	40
PC1_400	-	1.23	0.61	0.5546	1.50	-	40
PC2_400	-	0.87	0.43	0.6714	1.06	-	40
PC3_400	-	1.57	0.78	0.4467	1.91	-	40
River400_sqrt	-	0.40	0.19	0.8564	0.48	-	40
PC1_1000	-	1.44	0.71	0.4873	1.75	-	40
PC2_1000	-	9.12	5.01	0.0091*	11.13	-	40
PC3_1000	-	0.10	0.05	0.9414	0.13	-	40
River1000_sqrt	-	0.48	0.24	0.8026	0.59	-	40
Sequential tests for 100 m buffer							
Prox_Essel_sqrt	15.179	27.59	20.29	0.0001*	33.650	33.65	40
+ BirdCount_sqrt	13.837	4.55	3.56	0.0338*	5.546	39.20	39
Sequential tests for 400 m buffer							
Prox_Essel_sqrt	15.179	27.59	20.29	0.0001*	33.65	33.65	40
+ BirdCount_sqrt	13.837	4.55	3.56	0.0338*	5.55	39.20	39
Sequential tests for 1000 m buffer							
Prox_Essel_sqrt	15.179	27.59	20.29	0.0001*	33.65	33.65	40
+ BirdCount_sqrt	13.837	4.55	3.56	0.0338*	5.55	39.20	39

Table 9. Test statistics of distance-based linear models (DISTLMs) investigating the relationships between the movement into wetland sites (once controlled for effort) and the individual predictor variables. The marginal tests show the individual relationships between the predictor variables and the response. The sequential tests show the variables selected by the stepwise selection procedure based on AICc selection criteria. "SS" is the sum of squares, *F* is the pseudo-F statistic, p_{perm}, is the p-value, "Var. (%)" is the percentage of variation explained and "Cum. var. (%)" is the cumulative percentage of variation explained. Asterisks indicate predictors explaining a significant proportion of variation in the response variable (α = 0.05).

Variable Group	AICc	SS	*F*	p_{perm}	Var (%)	Cum. Var (%)	Residual df
Marginal tests							
Prox_Essel_sqrt	-	12.86	18.29	0.0001*	31.38	-	40
WetlandSize_log	-	0.09	0.09	0.7701	0.21	-	40
WeaverCount2013	-	2.52	2.62	0.1067	6.15	-	40
BirdCount_sqrt	-	2.63	2.74	0.1070	6.41	-	40
PC1_100	-	0.55	0.54	0.4972	1.34	-	40
PC2_100	-	0.25	0.24	0.5832	0.60	-	40
PC3_100	-	2.18	2.25	0.1466	5.32	-	40
River100_sqrt	-	0.01	0.01	0.9329	0.02	-	40
PC1_400		0.05	0.05	0.8401	0.11	-	40
PC2_400		0.07	0.07	0.8014	0.17	-	40
PC3_400		1.46	1.48	0.2191	3.57	-	40
River400_sqrt		0.39	0.39	0.5695	0.95	-	40
PC1_1000	-	0.47	0.47	0.4995	1.16	-	40
PC2_1000	-	4.87	5.39	0.0246*	11.88	-	40
PC3_1000	-	0.06	0.06	0.7871	0.16	-	40
River1000_sqrt	-	0.48	0.47	0.5071	1.16	-	40
Sequential tests for 100 m buffer							
Prox_Essel_sqrt	-12.519	12.86	18.29	0.0001*	31.38	31.38	40
+ WeaverCount2013	-14.945	3.01	4.67	0.0388*	7.34	38.72	39
+ BirdCount_sqrt	-15.806	1.90	3.12	0.0827	4.65	43.36	38
Sequential tests for 400 m buffer							
Prox_Essel_sqrt	-12.519	12.86	18.29	0.0001*	31.38	31.38	40
+ WeaverCount2013	-14.945	3.01	4.67	0.0388*	7.34	38.72	39
+ BirdCount_sqrt	-15.806	1.90	3.12	0.0827	4.65	43.36	38
Sequential tests for 1000 m buffer							
Prox_Essel_sqrt	-12.519	12.86	18.29	0.0001*	31.38	31.38	40
+ WeaverCount2013	-14.945	3.01	4.67	0.0388*	7.34	38.72	39
+ BirdCount_sqrt	-15.806	1.90	3.12	0.0827	4.65	43.36	38

Table 10. Test statistics of distance-based linear models (DISTLM) investigating the relationships between the movement out of wetland sites (once controlled for effort) and the individual predictor variables. The marginal tests show the individual relationships between the predictor variables and the response. The sequential tests show the variables selected by the stepwise selection procedure based on AICc selection criteria. "SS" is the sum of squares, *F* is the pseudo-F statistic, p_{perm}, is the p-value, "Var. (%)" is the percentage of variation explained and "Cum. var. (%)" is the cumulative percentage of variation explained. Asterisks indicate predictors explaining a significant proportion of variation in the response variable (α = 0.05).

Variable Group	AICc	SS	*F*	p_{perm}	Var (%)	Cum. Var (%)	Residual df
Marginal tests							
Prox_Essel_sqrt	-	14.73	22.43	0.0001*	35.92	-	40
WetlandSize_log	-	0.03	0.03	0.8617	0.08	-	40
WeaverCount2013	-	0.08	0.08	0.7843	0.19	-	40
BirdCount_sqrt	-	1.92	1.96	0.1744	4.68	-	40
PC1_100	-	1.31	1.32	0.2641	3.19	-	40
PC2_100	-	0.55	0.55	0.4650	1.35	-	40
PC3_100	-	0.23	0.22	0.6377	0.55	-	40
River100_sqrt	-	0.71	0.71	0.4044	1.74	-	40
PC1_400_std	-	1.19	1.19	0.2760	2.89	-	40
PC2_400_std	-	0.80	0.80	0.3763	1.95	-	40
PC3_400_std	-	0.11	0.10	0.7422	0.26	-	40
River400_sqrt_std	-	0.01	0.01	0.9405	0.01	-	40
PC1_1000	-	0.96	0.96	0.3330	2.35	-	40
PC2_1000	-	4.25	4.63	0.0361*	10.38	-	40
PC3_1000	-	0.04	0.04	0.8492	0.10	-	40
River1000_sqrt	-	0.01	0.01	0.9327	0.02	-	40
Sequential tests for 100 m buffer							
Prox_Essel_sqrt	-15.398	14.73	22.43	0.0001*	35.92	35.92	40
+ BirdCount_sqrt	-16.209	1.89	3.02	0.0889	4.61	40.53	39
Sequential tests for 400 m buffer							
Prox_Essel_sqrt	-15.398	14.73	22.43	0.0001*	35.92	35.92	40
+ BirdCount_sqrt	-16.209	1.89	3.02	0.0927	4.61	40.53	39
+ PC2_400	-17.36	2.00	3.40	0.0716	4.89	45.42	38
Sequential tests for 1000 m buffer							
Prox_Essel_sqrt	-15.398	14.73	22.43	0.0001*	35.92	35.92	40
+ BirdCount_sqrt	-16.209	1.89	3.02	0.0927	4.61	40.53	39

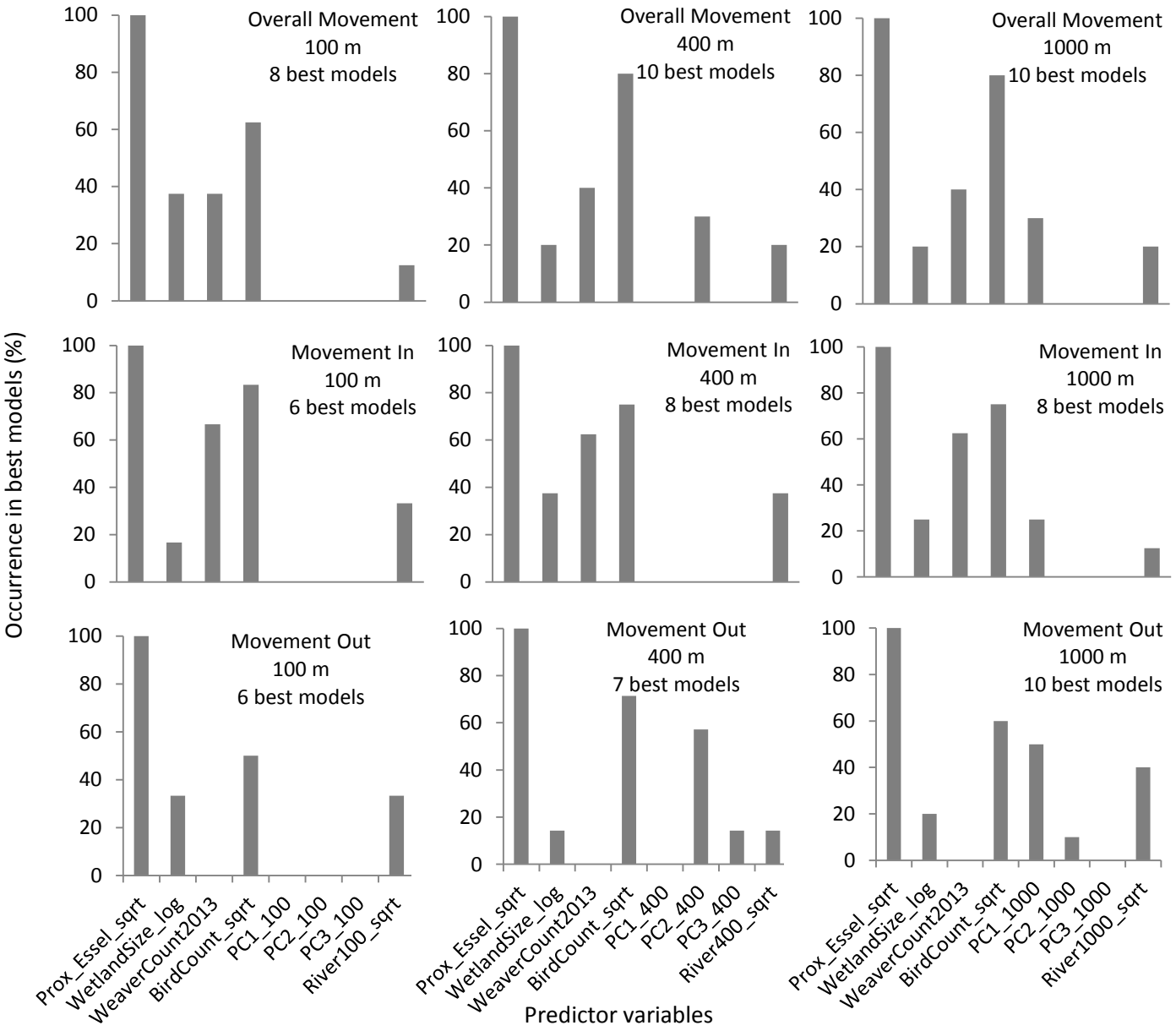

Figure 3. Presence of each predictor variable in each set of best models for overall movement, movement in and movement out at all three spatial scales (100 m, 400 m, 1000 m) as a percentage of the total number of best models. The best models were determined through distance-based linear models (DISTLMs) using the "best" selection procedure and the AICc selection criteria. The best models were within 2 AICc units of the most parsimonious models and are therefore worth considering as completive models.

Table 11. Component loadings produced by principal components analysis (PCA) on the proportions of different land use types within the three buffer sizes (100 m, 400 m, 1000 m). The percentage variation, and cumulative percentage variation, explained by principal component axes with eigenvalues >1 is shown.

	100 m buffers			400 m buffers			1000 m buffer		
Variable	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Urban_Residential	0.74	-0.04	0.21	-0.71	-0.18	0.25	-0.62	0.01	0.53
Urban_Industrial	-0.23	0.74	-0.31	0.45	-0.61	-0.33	-0.26	0.26	-0.81
Vegetation_Natural	-0.59	-0.12	0.44	0.49	0.46	0.27	0.44	-0.60	-0.07
Vegetation_Planted	-0.20	-0.44	0.19	0.18	0.01	0.74	-0.15	-0.63	-0.09
Waterbodies and wetlands	-0.09	-0.48	-0.79	-0.14	0.62	-0.46	0.57	0.43	0.24
Eigenvalues	1.32	1.13	1.03	1.27	1.19	1.09	1.28	1.19	1.10
Variation (%)	0.35	0.25	0.21	0.32	0.28	0.24	0.33	0.28	0.24
Cumm. Variation (%)	0.35	0.60	0.81	0.32	0.61	0.84	0.33	0.61	0.85

Discussion

This study used mark-release-recapture records to investigate the possible influence that proximity, site characteristics and the nature of the urban matrix surrounding sites may have had on weaver birds moving into and out of wetlands in Cape Town, South Africa. Site proximity was the dominant predictor explaining weaver movement and had a significant and positive relationship with both movement into and out of wetland sites. Once the large portion of variation in movement explained by proximity was accounted for, the features of the sites themselves, which estimated patch size and quality, did not have an overwhelmingly strong influence on weaver movement. Although patch size did not have a clear influence on movement, more detailed statistical tests revealed that the number of weavers and the number of birds at the sites may be important variables to consider. The primary interest of this study was to investigate whether aspects of the urban matrix affected weaver movement and although there was weak evidence for some aspects being influential, overall the matrix did not have a significant effect on weaver movement.

Site proximity promotes weaver movement

In their simulation of animal dispersal, Gustafson and Gardner (1996) found that increased proximity was associated with higher rates of movement and this finding corresponds with one of the pillars of island biogeography theory; patches that are closer together will experience more exchange of individuals than will more isolated patches (MacArthur & Wilson 1967). A well connected patch (high proximity) would be more likely to receive immigrants than a poorly connected patch (no nearby neighbours) not only because having more neighbours increases the number of possible "sources" for immigration, but also because the risks of arriving at a patch are lower if the distances between it and other patches are short (Fleishman et al. 2002; Bowler & Benton 2005; Hodgson et al. 2011). Animals may be more likely to leave a patch if they are aware of a neighbouring patch and the probability that they are aware of such neighbours might be greater if they are within searching distance of the current patch. Emigration might therefore be positively affected by site proximity (Bowler & Benton 2005).

The finding that weaver movement is strongly affected by proximity may not be surprising, but it could have important conservation implications. Maintaining a degree of mixing is essential for the persistence of fragmented populations (Simberloff & Cox 1987; Crooks & Sanjayan 2006) and if the exchange of individuals is affected by the proximity of patches, then it is important to maintain, if not improve, this aspect of the landscape and to avoid further isolation. Removing or destroying wetland habitats might increase isolation of remaining habitats and reduce landscape connectivity. It is therefore important to avoid such habitat loss. For example, if the proposal to build a shopping mall on Princess Vlei (one of Cape Town's biggest wetlands and also the location of two of my sites) (Princess Vlei Forum, see: http://www.princessvlei.org) is successful, not only will it result in habitat loss but could also increase the level of isolation in the system, potentially affecting connectivity. Ensuring habitat connectivity is also important at the community level, since well-connected patches

tend to have higher biomass and species richness than isolated patches (Prugh et al. 2008), which is certainly desirable in a potential depauperate urban setting.

Wetland size does not strongly influence weaver movement, but habitat quality might be important

Once the variation in movement explained by proximity was accounted for, the site variables contributed marginally in explaining any further variation, indicating that as a group, the site variables were not exceptionally important predictors. Their inclusion in the stepwise selected models, and varying presence in the "best" models, however, suggested that some of these variables may have had an influence on weaver movement. Apart from the lack of weaver colony size in the models explaining movement out of sites, there was no overwhelming difference in the variables included in the models explaining movement out of and movement into sites, suggesting that weaver movement into and out of sites might be similarly influenced by these site variables.

The degree of movement into and out of a patch could be influenced by patch size as animals may be encouraged to leave small, unproductive patches in search of larger, more profitable patches which, due to their size, may be also easier to find (Bowler & Benton 2005). In the present study however, wetland size did not emerge as a strong predictor of weaver movement as it was not selected in the stepwise selected models nor did it appear in many of the best models. Although weavers prefer to nest and breed over water for safety (Hockey et al. 2005), they are not water birds and the size of the wetlands with which they are associated may be less important than the area of vegetation that they directly utilise. An additional measurement of the area of utilised vegetation at each site (i.e.: reeds, over-hanging trees, etc.) would provide an alternative and possibly more useful measure of habitat patch size that could be incorporated into future studies of this nature.

In studying the movement behaviour of collared pikas (*Ochotona collaris),* Franken and Hik (2004) found that these animals wouldn't typically move into patches that lacked conspecifics and postulated that the presence of conspecifics was an indication of patch suitability which could

influence an immigration decision. The number of weavers seen at the sites in 2013 was a significant predictor in the most parsimonious model explaining movement into the sites and frequently appeared in corresponding sets of best models. However, this variable was not included in the stepwise selected model explaining movement out of sites and never appeared in any of these sets of best models. The presence of conspecifics might indicate to dispersing weavers the quality of the site and may influence their decision to enter it. Weavers are colonial birds (Hockey et al. 2005) that would benefit from a colony of a particular size and this too could be influencing their movement into sites (Bowler & Benton 2005). Indeed, colonial lesser kestrels (*Falco naumanni*) have been observed to move out of patches with small colonies and into patches with larger colonies more often than the other way around (Serrano et al. 2005).

The number of birds counted at the sites in 2013 was included in the most parsimonious model for each analysis and also in most of the comparatively parsimonious models for movement both in and out of sites, indicating that although this variable may not have been strictly significant in the stepwise selected models, it may still hold some predictive power. The number of birds present at the site may also be an indication, albeit a somewhat crude one, of a site's carrying capacity or quality (Johnson 2007), and might play a role in a weaver's decision to leave or enter a site (Bowler & Benton 2005). If weaver movement is indeed influenced by patch quality, then in the interest of maintaining landscape connectivity, Cape Town's wetlands should be managed accordingly by reducing pollution, discouraging littering and avoiding further habitat removal.

Point counts are a useful field method as they are relatively easy to conduct and can provide a snapshot of the bird community at a site. However, the instantaneous nature of point counts does not provide information about historical composition or abundance of birds and in this study, where weaver sampling was conducted over many years, such information would have been valuable. Due to the rapid alteration of landscapes often associated with urbanization, many of the sites have changed dramatically over the years, affecting the local bird communities and weaver colonies. For

example, two sites (Athlone Sewage Works and one in Marina Da Gama) had been entirely cleared of the reeds in which the weavers used to nest and by the time the counts were conducted, the weaver colonies were greatly reduced, if not all together absent. Habitat modification could have also similarly affected the rest of the local bird community. Thus, any influence of weaver colony size and bird count showed in the analyses should be interpreted with caution and not treated as causative. From these results, it is not possible to infer whether patch size or habitat quality had an influence on weaver movement and this highlights the need to develop a more realistic measure of habitat quality, especially since habitat quality is known to influence bird communities (Fleishman et al. 2002; Hodgson et al. 2011).

The urban matrix does not strongly impede or assist weaver movement

In a comprehensive review of ecological studies focussing on the effects that the matrix has on individuals, populations and communities, Prevedello and Viera (2010) concluded that although the nature of the matrix can be an important predictor, isolation and patch size "are the main determinants of ecological parameters in landscapes". The present study supports this generalization as proximity was the main predictor of movement and the overall effect of the urban matrix was negligible. The urban matrix variables, when grouped according to buffer radius, did not have a significant influence on weaver movement and the addition of these variable sets reduced model parsimony. This contrasts with Prevedello and Viera's (2010) finding that incorporating matrix effects can improve the explanatory power of ecological models. The inclusion of one of these variables in one of the stepwise selected models (explaining movement out of sites with a 400 m scale) and the appearance of some of the land use variables in the sets of comparatively parsimonious models suggested that individually, these variables may hold some predictive power. None of the land use variables measured within the 100 m buffer were present in the sets of "best" models, indicating that weaver movement was not affected by the urban matrix at the finest spatial scale. The proportions of industrial area, wetland area and planted vegetation measured within the

400 m buffers may have influenced weaver movement out of the sites. Weaver movement into and out of sites may also have been influenced by the proportional areas of residential land use, industrial land use, wetlands and natural vegetation measured within the 1000 m buffers. Further work, perhaps in the form of multimodal inferencing (Burnham & Anderson 2004), is needed to draw conclusions from these model comparisons, but from the analyses conducted here, it seems that although weaver movement is not significantly affected by the urban matrix in general, individual land uses may be marginally influential. Although it is not possible to infer causality from these results, they do point to the need for more detailed investigation into the impacts of these land cover types on bird movement in Cape Town.

The length of river within each buffer was included in the "buffer variables" to assess whether weavers potentially use rivers as movement corridors to enter and/or leave sites. Although river length was not included in the stepwise selected models, its appearance in the sets of most parsimonious models indicated that at all three scales, river length may have had an influence on weaver movement both into and out of the sites. The incorporation of direct observations and GPS tracking into future studies would strengthen the conclusions drawn from these types of results. If weavers are using rivers as a means to access and depart from wetlands then in the interest of maintaining connectivity, these rivers should be conserved. It is also noted that poorly managed urban rivers detract from the landscape's aesthetics, pose health risks to humans and diminish their potential as natural habitats (Findlay & Taylor 2006). Such reasons alone are sufficient in promoting the proper care and management of urban rivers but if it is found that birds use them as movement corridors, this would provide additional impetus for their conservation.

Weavers as generalist, "urban adapters" with a fragmented past

Considering the adaptive nature of weavers (Hockey et al. 2005), it is not surprising that they are not strongly affected by the urban matrix. McKinney (2002) proposed that animals (especially birds) living in an urban context can be categorised into three groups; "urban avoiders", "urban

adapters" and "urban exploiters" depending on the way they respond to urban land use. Urban avoiders are sensitive to urban land use and rely solely on natural resources, urban adapters are species that subsidise their use of natural resources with human resources, and urban exploiters are species that have become wholly dependent on the human environment (McKinney 2002). Weaver species are well known to benefit from humans by feeding from bird feeders, nesting over farm dams and garden ponds and indirectly by roosting in alien trees (especially in the absence of reeds) (Hockey et al. 2005). My visits to the weaver colonies confirmed these reports as I saw weavers nesting over a garden pond in Blouberg, in alien trees in Ottery, and above sewage treatment ponds in Strandfontein. In light of this evidence, I would place weavers in the category of "urban adapters" that are not particularly sensitive to human activity and can therefore easily navigate through the urban matrix.

Their adaptablity to urban settings and resources may also place weavers as generalists, as opposed to specialists. Generalists can make use of a wide range of land cover types and do not respond to habitat/non-habitat boundaries as strongly as might a specialist species (Bender & Fahrig 2005). Because they can successfully use different components of the urban matrix, weavers may perceive it as a more homogenous, less antagonistic landscape (Bender & Fahrig 2005) and thus have little problem moving through it.

Their robust and adaptive nature may explain weavers' resilience to the urban matrix, but this could also be in part explained by their long association with fragmented habitats. Weavers often nest and roost above water bodies for safety (Hockey et al. 2005) and water bodies (especially wetlands) are naturally scattered throughout the landscape and can be considered as "ecological islands surrounded by terrestrial environment" (Amezaga et al. 2002). Residing in a naturally fragmented system, weavers may have evolved to be vagile in order to move over non-habitat to reach favourable habitat patches, explaining their insensitivity towards the terrestrial urban matrix

(Fahrig 2007). Indeed, one of the few studies on weaver movement in the Cape mentions the Cape Weaver's ability to "fly fast and direct" over the landscape (Fry & Keith 2004).

These hypotheses could be investigated further with the use of a matrix-tolerance model that takes into account a species' ability to utilise transformed matrix habitats when determining its sensitivity to fragmentation (Gascon et al. 1999). These sorts of models can be used by city planners to determine how different land uses may influence the effective isolation of remaining habitat patches (Ricketts 2001).

Shortcomings of using a pre-existing dataset

The main drawback of the SAFRING dataset was that it was not collected with a specific study or analysis in mind, which resulted in uneven sampling efforts at the different sites. The preliminary analyses illustrated the massive and overwhelming effect that effort had in explaining variation in movement which justified the incorporation of effort in the response variables. Datasets such as these are clearly very valuable in studying animal movements and behavioural responses to the urban matrix, but should be collected more systematically to aid the development of more streamlined and effective analyses.

Future research opportunities

Since connectivity is a dynamic aspect of the landscape, and may have a dynamic influence on the species in question, it should not be viewed as a static phenomenon (Crooks & Sanjayan 2006). Temporal variation in a landscape is thought to affect metapopulation dynamics and including temporal variation in ecological models can improve their explanatory power (Fleishman et al. 2002). As mentioned earlier, the urban setting is constantly changing and this may not only affect bird populations at specific habitats, but also the way that birds navigate through the matrix over time (Gustafson & Gardner 1996). This study attempted to condense weaver movement over six years and explain the variation in this movement using a set of somewhat static predictor variables.

Although spatial scales were incorporated into the analyses, a more temporally dynamic approach would have greater power and might yield additional insights.

The approach of grouping the four weaver species together was justified by their shared habitat preferences and dispersal strategies (Hockey et al. 2005). However, this may have negated any finer differences between the species, such as the fact that the bishops can be more territorial than the weavers (Hockey et al. 2005). In the interest of gaining more detailed information on animal movement, future studies could examine the responses of each species separately based on the premise that even closely related species can perceive the same landscape differently (Ricketts 2001). Animals at different life history stages are known to react to the landscape differently (Ewers & Didham 2006) and this distinction in responses is thought to have consequences for population survival and dynamics (Pennington & Blair 2011). The SAFRING dataset contains information on the sex and age of each bird caught which could be included in future studies to compare the movement of juveniles and adults, and of males and females.

Conclusions

Effective conservation of urban biodiversity requires a community level approach that seeks to understand the responses of different plant and animal inhabitants to a dynamic and complex landscape (Marzluff & Ewing 2001; Fagan & Calabrese 2006; Pennington & Blair 2011). However daunting this task may be, conducting studies such as this will contribute to our knowledge of how animals perceive the urban matrix and how aspects of their ecology, such as dispersal, are affected by it. This study focused on a robust group of birds and found that although their movements may not be significantly affected by the nature of the urban matrix, nor by habitat size or quality, habitat proximity clearly influenced their perception of how connected the landscape is. Not only does this finding agree with island biogeography theory (MacArthur & Wilson 1967), but it also has potentially important conservation implications, and motivates to avoid further habitat loss as this is likely to decrease the connectivity between populations. A large portion of conservation research and effort

is focused on threatened and rare species as the risks of losing these species are so high, but there is also merit in studying and conserving common species, such as weavers, and I propose two benefits of doing so. Traditionally, the use of sensitive animals as "umbrella species" is recommended as managing the landscape for their specific needs may also have far-reaching benefits for other species (Fagan & Calabrese 2006). In this regard, weavers may not be ideal "umbrella species"; however, the finding that the movements of highly vagile and resilient species are affected by habitat proximity should spur the investigation into the responses of other, less resilient species to the urban landscape and encourage conservative conservation. Secondly, considering the conservation of common species will aid in keeping them common and also ensure their continued contribution to a biologically diverse landscape (Pennington & Blair 2011), which is especially important if they preform functional roles in the ecosystem (i.e. as abundant prey species). This study on weaver movement between wetlands in Cape Town not only contributes to our knowledge of urban biodiversity in a global biodiversity hotspot, but also highlights the need for further research into how other, less resilient species respond to this complex and ever changing landscape.

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Appendix

Appendix 1. Sets of models with the best parsimony for all the expanded proximity, site and buffer predictor variables associated with overall movement into and out of the wetland sites for the three spatial scales (100 m, 400 m, 1000 m). All the models were within 2 AICc values of the most parsimonious model and are listed in descending order of parsimony. These models were selected from all 8 possible predictor variables using distance-based linear models (DISTLM) using the "BEST" selection procedure based on AICc selection criteria. The amount of variation in the movement in and out (represented by a resemblance matrix) explained by each model is presented (%Var.), as is number of the predictor variables included in each model.

	AICc	% Var.	No. Vars	Variables
100 m	13.837	39.20	2	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt
	14.266	42.05	3	Proximity_Esselstyn_sqrt, Wetland Size_log, Birdcount2013_sqrt
	14.335	41.96	3	Proximity_Esselstyn_sqrt, WeaverCount2013 , Birdcount2013_sqrt
	15.1	37.39	2	Proximity_Esselstyn_sqrt, WeaverCount2013
	15.179	33.65	1	Proximity_Esselstyn_sqrt
	15.398	40.47	3	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, River_100_sqrt
	15.443	43.96	4	Proximity_Esselstyn_sqrt, Wetland Size_log, , WeaverCount2013, Birdcount2013_sqrt
	15.668	36.49	2	Proximity_Esselstyn_sqrt, Wetland Size_log
	AICc	% Var.	No.Vars	Variables
400 m	13.837	39.20	2	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt
	14.266	42.05	3	Proximity_Esselstyn_sqrt, Wetland Size_log, Birdcount2013_sqrt
	14.279	42.03	3	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, PC2_400
	14.335	41.96	3	Proximity_Esselstyn_sqrt, WeaverCount2013 , Birdcount2013_sqrt
	14.515	41.71	3	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, River_400_sqrt
	14.69	44.96	4	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt,PC2_400, River_400_sqrt
	14.949	44.62	4	Proximity_Esselstyn_sqrt, WeaverCount2013 , Birdcount2013_sqrt, PC2_400
	15.1	37.34	2	Proximity_Esselstyn_sqrt, WeaverCount2013
	15.179	33.65	1	Proximity_Esselstyn_sqrt
	15.443	43.96	4	Proximity_Esselstyn_sqrt, Wetland Size_log, WeaverCount2013, Birdcount2013_sqrt
	AICc	% Var.	No.Vars	Variables
1000 m	13.837	39.20	2	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt
	14.266	42.05	3	Proximity_Esselstyn_sqrt, Wetland Size_log, Birdcount2013_sqrt
	14.335	41.96	3	Proximity_Esselstyn_sqrt, WeaverCount2013, Birdcount2013_sqrt
	14.774	41.35	3	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt. PC1_1000
	15.1	37.34	2	Proximity_Esselstyn_sqrt,WeaverCount2013
	15.14	44.37	4	Proximity_Esselstyn_sqrt, WeaverCount2013, Birdcount2013_sqrt, PC1_1000
	15.179	44.62	1	Proximity_Esselstyn_sqrt
	15.276	40.64	3	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, River_1000_sqrt
	15.443	43.96	4	Proximity_Esselstyn_sqrt, Wetland Size_log, WeaverCount2013, Birdcount2013_sqrt
	15.519	43.86	4	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, PC1_1000, river_1000

Appendix 2. The sets of models with the highest parsimony for all the expanded proximity, site and buffer predictor variables associated with movement into the wetland sites for the three spatial scales (100 m, 400 m, 1000 m). All the models were within 2 AICc values of the most parsimonious model and are listed in descending order of parsimony. These models were selected from all 8 possible predictor variables using distance-based linear models (DISTLM) using the "BEST" selection procedure based on AICc selection criteria. The amount of variation in the movement in and out (represented by a resemblance matrix) explained by each model is presented (%Var.), as is number of the predictor variables included in each model.

	AICc	% Var	No. Vars	Variables
100 m	-15.806	43.36	3	Proximity_Esselstyn_sqrt, WeaverCount2013, Birdcount2013_sqrt
	-14.945	38.715	2	Proximity_Esselstyn_sqrt, WeaverCount2013
	-14.363	37.859	2	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt
	-14.266	44.752	4	Proximity_Esselstyn_sqrt, WetlandSize_log, WeaverCount2013, Birdcount2013_sqrt
	-14.113	41.03	3	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, River_100_sqrt
	-13.603	43.874	4	Proximity_Esselstyn_sqrt, WeaverCount2013, Birdcount2013_sqrt, River_100_sqrt
	AICc	% Var	No.Vars	Variables
400 m	-15.806	43.36	3	Proximity_Esselstyn_sqrt, WeaverCount2013, Birdcount2013_sqrt
	-15.525	46.384	4	Proximity_Esselstyn_sqrt, WeaverCount2013, Birdcount2013_sqrt, River_400
	-15.45	42.878	3	Proximity_Esselstyn_sqrt, WeaverCount2013, River_400_sqrt
	-14.945	38.715	2	Proximity_Esselstyn_sqrt, WeaverCount2013
	-14.363	37.859	2	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt
	-14.266	44.752	4	Proximity_Esselstyn_sqrt, WetlandSize_log, WeaverCount2013, Birdcount2013_sqrt
	-14.113	41.03	3	Proximity_Esselstyn_sqrt, WetlandSize_log, Birdcount2013_sqrt
	-14.083	44.511	4	Proximity_Esselstyn_sqrt, WetlandSize_log, Birdcount2013_sqrt, River_400_sqrt
	AICc	% Var	No.Vars	Variables
1000 m	-15.806	43.36	3	Proximity_Esselstyn_sqrt, WeaverCount2013, Birdcount2013_sqrt
	-15.117	45.861	4	Proximity_Esselstyn_sqrt, WeaverCount2013, Birdcount2013_sqrt, PC1_1000
	-14.945	38.715	2	Proximity_Esselstyn_sqrt, WeaverCount2013
	-14.383	44.906	4	Proximity_Esselstyn_sqrt, WeaverCount2013, Birdcount2013_sqrt, River_1000_sqrt
	-14.363	37.859	2	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt
	-14.266	44.752	4	Proximity_Esselstyn_sqrt, WetlandSize_log, WeaverCount2013, Birdcount2013_sqrt
	-14.113	41.03	3	Proximity_Esselstyn_sqrt, WetlandSize_log, Birdcount2013_sqrt
	-13.915	40.752	3	Proximity_Esselstyn_sqrt, WeaverCount2013, PC1_1000

Appendix 3. The sets of models with the highest parsimony for all the expanded proximity, site and buffer predictor variables associated with movement out of the wetland sites for the three spatial scales (100 m, 400 m, 1000 m). All the models were within 2 AICc values of the most parsimonious model and are listed in descending order of parsimony. These models were selected from all 8 possible predictor variables using distance-based linear models (DISTLM) using the "BEST" selection procedure based on AICc selection criteria. The amount of variation in the movement in and out (Euclidean distance matrix) explained by each model is presented (%Var.), as is number of the predictor variables included in each model.

	AICc	% Var	No. Vars	Variables
100 m	-16.209	40.531	2	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt
	-15.593	43.072	3	Proximity_Esselstyn_sqrt, Wetland Size_log, Birdcount2013_sqrt
	-15.398	35.923	1	Proximity_Esselstyn_sqrt
	-15.2	39.085	2	Proximity_Esselstyn_sqrt, River_100_sqrt
	-14.88	42.098	3	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, River_100_sqrt
	-14.86	38.59	2	Proximity_Esselstyn_sqrt, Wetland Size_log
	AICc	% Var	No.Vars	Variables
400 m	-17.36	45.417	3	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, PC2_400
	-16.209	40.531	2	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt
	-16.002	40.238	2	Proximity_Esselstyn_sqrt, PC2_400
	-15.973	46.952	4	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, PC2_400, River_400_sqrt
	-15.593	43.072	3	Proximity_Esselstyn_sqrt, Wetland Size_log, Birdcount2013_sqrt
	-15.398	35.923	1	Proximity_Esselstyn_sqrt
	-15.189	45.953	4	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, PC2_400, PC3_400
	AICc	% Var	No.Vars	Variables
1000 m	-16.245	47.295	4	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, PC1_1000, river_1000_sqrt
	-16.209	40.531	2	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt
	-15.593	43.072	3	Proximity_Esselstyn_sqrt, Wetland Size_log, Birdcount2013_sqrt
	-15.401	42.811	3	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, PC1_1000
	-15.398	35.923	1	Proximity_Esselstyn_sqrt
	-14.962	38.739	2	Proximity_Esselstyn_sqrt, PC1_1000
	-14.86	38.59	2	Proximity_Esselstyn_sqrt, Wetland Size_log,
	-14.457	41.512	3	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, River_1000_sqrt
	-14.357	41.372	3	Proximity_Esselstyn_sqrt, PC1_1000,river_1000 _sqrt
	-14.347	48.333	5	Proximity_Esselstyn_sqrt, Birdcount2013_sqrt, PC1_1000, PC2_1000, river_1000_sqrt